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COMPENSATORY REACTIONS OF POPULATIONS TO STRESSES, AND THEIR EVOLUTIONARY SIGNIFICANCE

By A. J. Nicholson[*]

[*Manuscript received February* 15, 1954]

Summary

Cultures of *Lucilia cuprina* which were subjected to different kinds and intensities of stress automatically accommodated themselves to these stresses and maintained themselves in a state of balance under all the varied environmental conditions provided.

Compensatory reaction always counteracted in some degree the adverse effects of the stresses to which the insects were subjected. Thus the persistent destruction of a particular age-group always caused more individuals to reach this age, so reducing the effects produced by destruction upon population density.

It is shown that density governed compensatory reaction is a necessary counterpart of selection in evolutionary progress.

I. Introduction

Organisms of all kinds multiply when conditions are favourable, and their populations inevitably dwindle to extinction when conditions are persistently unfavourable. In spite of these characteristics, populations of the same species are observed to persist without progressive increase or decrease in different places in which environmental conditions are far from identical. It is evident therefore that some mechanism must operate which brings about an adjustment between the ability of the organisms to multiply and the resistance of the various environments occupied, such that the one counteracts the other and so prevents progressive population change.

Chapman (1931) in his theory of "biotic potential" postulated that the properties of organisms are adjusted to the inherent resistance of the environment and (by implication) that this was brought about by some evolutionary process. Apart from the fact that such an equilibrium between inherent properties would be sustained at any density, and so could not adjust population densities in relation to environmental conditions, it would be necessary for the properties of a species to vary in precise relation to the varied conditions in the different parts of the range of the species. That the genetical compositions of populations of the same species do often vary considerably from place to place is now well known; but natural selection (which governs these compositions) could not possibly produce and preserve the precise adjustment postulated. To do so it would often be required to operate in reverse by selectively destroying any abnormally potent individuals which appeared; for the preservation of

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these at the expense of the previously normal individuals by the characteristic process of selection would lead to progressive and indefinite population growth, in the absence of some other mechanism with a compensatory influence.

Table 1

EFFECTS PRODUCED IN POPULATIONS OF *LUCILIA CUPRINA* BY THE DESTRUCTION OF DIFFERENT CONSTANT PERCENTAGES OF EMERGING ADULTS

The populations were limited by the provision of only 0·5 g of ground liver for the adults per day in each culture; water and sugar for the adults, and the food for the larvae (from which the adults were excluded) was supplied in excess of requirements at all times

AVERAGES OF OBSERVED QUANTITIES

Situation	Imposed Destruction of Emerging Adults *a*	Pupae Produced per Day *b*	Adults Emerged per Day *c*	Adults Destroyed per Day *d*	Accessions Of Adults per Day *e*	Natural Deaths of Adults per Day *f*	Mean Adult Population *g*
A	**0**	624	**573**	0	573	573	**2520**
B	**50%**	782	**712**	356	356	356	**2335**
C	**75%**	948	**878**	658	220	220	**1588**
D	**90%**	1361	**1260**	1134	126	125	**878**

DERIVED CHARACTERISTICS OF THE POPULATIONS

Situation	% of Total Mortality Due to:			Mean Adult Life Span (days) $k = g/e$	Mean Birth-rate (per individual per day) $l = b/g$	Mean Coefficient of Fertility $m = b/e = kl$	Minimum Coefficient of Replacement $n = \frac{100}{100 - a} = c/e$
	Pupal Mortality $h = \frac{100(b-c)}{b}$	Imposed Destruction $i = \frac{100d}{b}$	Natural Deaths of Adults $j = \frac{100f}{b}$				
A	8·2	0	**91·8**	4·4	0·25	**1·1**	1
B	8·9	45·5	**45·5**	6·6	0·33	**2·2**	2
C	7·3	69·4	**23·2**	7·2	0·60	**4·3**	4
D	7·4	83·3	**9·2**	7·0	1·55	**10·8**	10

II. Experimental

In order to investigate this problem of adjustment, many laboratory populations of the Australian sheep blowfly, *Lucilia cuprina* Wied., have been subjected to different kinds and degrees of stress. As the results obtained clearly demonstrate the existence and characteristics of an efficient mechanism which compensates for variations of the environment, and as they have an important bearing upon many biological problems, it has been decided to present here a brief account of the pertinent results of some of the experiments. A full account of these and other similar experiments will be published in a series of papers later.

The essential feature of these experiments was that the populations were left free to develop and to maintain themselves under predetermined environmental conditions for long periods, generally about a year. Apart from keeping daily records, the only action taken was the maintenance of the selected environmental conditions. This consisted mainly of providing a continuous supply of food and water in appropriate quantities for the insects, and, in some experiments, of destroying insects at a selected stage of development in accordance with a particular and invariable plan. All cultures were maintained at a constant temperature of 25°C. In all the analyses given here, records of the populations during the first few weeks when they were clearly influenced by the initial conditions are omitted from consideration, for the temporary influence of initial conditions is not pertinent to present considerations.

Table 1 presents an analysis of the results obtained in a set of concurrent experiments in which the populations were limited by restricting the supply of ground liver for the adults to 0.5 g per day in each culture, water and sugar for the adults, and larval food being supplied in excess. This restriction did not directly influence the mortality of the adults, for other experiments have shown clearly that adults supplied with only water and sugar live at least as long as do adults supplied with ground liver as well. But it did influence natality, for the greater the number of adults competing for the limited supply of liver the smaller is the amount obtained on the average by an individual, and so smaller numbers of individuals obtain sufficient for the development of eggs—adults of *L. cuprina* being incapable of developing eggs unless they obtain adequate quantities of protein.

The consequent inverse relation between population size and egg production is seen by comparison of columns *g* and *b* in Table 1 (for it is known that the mortality of larvae is negligible in cultures supplied with excess larval food, and so the number of pupae represents the number of viable eggs laid). The imposed destruction of emerging adults reduced the severity of competition amongst the adults for the limited supply of liver, and so increased their fertility, as shown in column *m*. If mortality were wholly due to the imposed destruction and the natural deaths of adults, the number of offspring an individual would be required to produce on the average in its lifetime as replacements for those dying from these known causes is shown in column *n*. Actually the fertility (*m*) was greater than this, for there was a somewhat erratic pupal mortality (due to unknown causes) for which the population also compensated automatically by a further increase in fertility.

It will be observed that the increase of the coefficient of fertility (*m*) with increasing destruction was not wholly due to the increase in birth-rate (*l*) caused by the adults obtaining more adequate quantities of liver, but was in part due to an increase in the average life span (k) of the adults. This was due to a lessening of the adverse effect of adult crowding in the cages in which the populations were reduced by imposed destruction. So, although the per-

TABLE 2

EFFECTS PRODUCED IN POPULATIONS OF *LUCILIA CUPRINA* BY THE VARIOUS ENVIRONMENTAL STRESSES INDICATED IN THE FIRST COLUMN

The populations were limited by the provision of only 50 g of larval food per day in each culture; ground liver (except in *J*), water, and sugar for the adults were supplied in an excess of requirements at all times

AVERAGES OF OBSERVED QUANTITIES

Situation	Imposed Destruction of Emerging Adults a	Larvae Hatched per Day b	Adults Emerged per Day c	Adults Destroyed per Day d	Accessions of Adults per Day e	Natural Deaths of Adults per Day f	Mean Adult Population g
E: Control cultures (no imposed destruction)	**0**	8794	**157**	0	157	157	**1252**
F Constant % of	**75%**	4121	**192**	144	48	48	**464**
G emerging adults	**95%**	1921	**437**	415	22	22	**249**
H destroyed	**99%**	1330	**909**	900	9	9	**128**
I: Bad oviposition site	**0**	4261	**234**	0	234	235	**1667**
J: Ground liver for adults restricted to 1 g per day	**0**	981	**598**	0	598	599	**4042**

DERIVED CHARACTERISTICS OF THE POPULATIONS

Situation	% of Total Mortality Due to:			Mean Adult Life Span (days)	Mean Birth-rate (per individual per day)	Mean Coefficient of Fertility	Minimum Coefficient of Replacement
	Larval Competition $h = \frac{100(b-c)}{b}$	Imposed Destruction $i = \frac{100d}{b}$	Natural Deaths of Adults $j = \frac{100f}{b}$	$k = g/e$	$l = b/g$	$m = b/e = kl$	$n = \frac{100}{100 - a} = c/e$
E	**98·2**	0	**1·8**	7·9	7·0	**55·8**	1
F	**95·3**	3·5	**1·2**	9·7	8·9	**85·8**	4
G	**77·3**	21·6	**1·1**	11·4	7·7	**88·0**	20
H	**31·6**	67·7	**0·7**	14·1	10·4	**146·3**	100
I	**94·5**	0	**5·5**	7·1	2·6	**18·2**	1
J	**39·0**	0	**61·0**	6·8	0·24	**1·6**	1

centage of individuals reaching maturity (*j*) varied approximately directly with the percentage $(100 - a)$ of flies not destroyed by the imposed factor, the mean adult population (*g*) varied to a lesser degree, for the surviving adults lived longer and produced more offspring, so in large measure countering the population-reducing influence of imposed destruction.

In the experiments recorded in situations *E-H* (Table 2), constant percentages of emerging adults were destroyed, just as in those recorded in Table 1, the difference being that in these experiments it was the restriction of the larval food supply which limited the populations. Note that, as in Table 1, increasing destruction of emerging adults led to an increased daily emergence of adults (Table 2*c*). The cause of this was the reduced larval competition for food which resulted from fewer eggs being laid (*b*) by the populations (*g*) which were reduced in numbers by the imposed destruction; for, as has already been shown (Nicholson 1948), the number of adults produced from a unit quantity of larval food increases with decreasing larval density, provided this is above a certain critical low level. Although place was made for the imposed destruction predominantly by reduction in the effects of larval competition (*h*), it was in part due to a reduction of mortality due to natural deaths of adults (*j*). The reduction of larval competition resulting from imposed destruction had two distinct effects: it increased the number of individuals (*c*) surviving the competitive stage, and it increased the size and vigour of the survivors. The latter effect was dominantly responsible for the observed increase in the coefficient of fertility (*m*), for the larger and more vigorous individuals produced more offspring (*l*) and lived longer (*k*), although the reduced crowding of the adults undoubtedly contributed to the increased life span. In these experiments, then, compensation for imposed destruction was due to a combination of reduced larval competition, lessened direct effects of adult crowding, and increased fertility, all these being reactive effects of the destruction.

The ability of populations of *L. cuprina* to preserve themselves in spite of severe stresses was also demonstrated by other experiments in which different systems of destruction were used, or in which different life stages were destroyed. Sometimes the compensation was even more marked than in situations *E-H*. For example, the destruction of 50 per cent. of the total adult population every second day produced no significant change in the mean adult population compared with a similar culture in which there was no imposed destruction; and in another experiment the destruction of 50 per cent. of all eggs laid more than doubled the mean adult population, compared with a control culture.

Compensation for the effects of factors adverse to individuals other than exposure to destruction was also demonstrated. In situation *I*, for example, the adults, while being given excess ground liver for their own use, were excluded from the larval food and had to lay their eggs through plastic gauze which did not permit their ovipositors to touch this food. In consequence their oviposition rate (*l*), and so also their coefficient of fertility (*m*), were greatly reduced. Because of this, the adult population automatically reached the comparatively high mean level (compare g in *E* and *I*) necessary to cause sufficient larval competition to destroy the surplus offspring produced. In situation *J* the mechanism of compensation is much the same, but the increase of the adult population due to a factor adverse to the individuals is even greater than in *I*. In this experiment there was a restriction of the daily supply of ground liver for the adults to 1 g, in addition to the restriction of the larval food supply to 50 g. Limitation of the population was dominantly due to adult competition for food which severely restricted oviposition (*l*), and in consequence there was a great reduction of larval competition (*h*). That is to say, a comparatively small part of the larval food was wasted by individuals which obtained insufficient to mature, and so an exceptionally large part of it was used effectively in the production of adults (compare *g* in *E* and *J*).

III. Discussion

In all the experiments discussed (except *H* and *J*) the populations oscillated in numbers fairly regularly and often very violently, the maxima in some being hundreds of times as large as the minima. An example, very similar to *E*, has already been illustrated (Nicholson 1950), and the mechanism of oscillation was briefly described: the right kind of reaction to cause an approach to the equilibrium density is always engendered by density change but, because of developmental lag, it causes the population to overshoot or undershoot this density, so causing a new displacement of density. A notable feature of oscillating populations is an alternation in time of a great excess of adult accessions over adult deaths, and of a great excess of adult deaths over accessions. In spite of this, comparison of columns *e* and *f* in the two tables shows that, when taken over a long period, the mean number of accessions equals the mean number of deaths in all situations. Moreover, other experiments have shown that the mean sizes of populations are directly proportional to the amount of the limiting requisite supplied; so it is clear that such populations are in a state of balance with their environments, in spite of their violent changes. They are systems governed and maintained in being by reaction, which not only opposes any departure from their equilibrium densities, but also compensates for any external stresses to which they may be exposed, provided these lie within the wide limits of tolerance determined by the characteristics of the populations.

The recorded experiments all deal primarily with population limitation due to the reactive effects of depletion of food; but there can be little doubt similar compensatory reaction should result from the depletion of any other kind of requisite. Even in these experiments the reactive effects of adult crowding (that is, of competition for living space) upon mortality and fecundity are evident; and it is clear from the kind of reaction recorded that, in the absence of other reactive factors, this would itself compensate for adverse influences by changes in the limiting degree of crowding. Moreover, the observed compensation for destruction which is characterized by an increase in the density of the age-group immediately preceding the one subject to destruction, and by increases and decreases in the densities of other age-groups, is in conformity with conclusions reached elsewhere concerning the effects produced by subjecting a host population governed by the action of a parasite species to an additional destructive factor (Nicholson 1933, conclusions 9, 17, and 18; Nicholson and Bailey 1935, conclusions 16, 17, 18, 31, and 32).

The fact that the persistent use of control measures against pests leads to the maintenance of their populations at new and generally lower levels, instead of causing progressive diminution in the densities of the pests, shows that compensatory reaction to external stresses is also a characteristic of populations living under field conditions. Clearly the imposed destruction in the new situations does not add to the mortality of the pests, for this must be 100 per cent. in any situation in which there is neither progressive increase nor progressive decrease. Evidently the reactive factors which previously held the pests in check at high levels relax their influence, so making place for the new destruction.

How populations automatically adjust themselves to a new destructive factor by a redistribution of mortality amongst the various factors which cause it is shown by Tables 1 and 2, for the sum of h, i, and j in all situations equals 100 per cent., and the result of this adjustment is that the populations are not reduced in proportion to the new destruction—in fact in some situations they may be increased.

IV. EVOLUTIONARY SIGNIFICANCE

Compensatory reaction of the kind revealed by these experiments enables populations of the same species to maintain themselves indefinitely under conditions which vary greatly in space and in time, at densities determined by the prevailing conditions and the properties of the animals; but note that only factors which oppose population growth with increasing intensity as density increases can limit populations and hold them in a state of balance with their environments—although factors which do not change in intensity with density may profoundly influence the densities at which the reactive factors adjust the populations, as is shown by the effects of destruction at constant percentages in Tables 1 and 2. Because of this compensatory mechanism, populations commonly exist in a condition of great security (except near their limits of distribution); for in most places the resistance of the environment consists largely of reaction to their own densities, and this is automatically relaxed when they are subjected to new stresses.

By contrast, the genetical composition of a population is in a state of extreme instability, for any persistent change which differentially affects the potency of individuals leads to the complete replacement of the less potent individuals by those which have even a slight advantage, provided this advantage is inherited by the offspring as a single factor. If the greater potency is due to a particular combination of genes, the appearance of individuals possessing it leads to a new equilibrium gene ratio. Such change in the properties of the population is caused by the automatic adjustment of environmental reaction to an intensity which just counterbalances the *average* properties of the individuals. Consequently the induced environmental resistance is insufficient to prevent progressive increase of the more potent individuals; and, as intensity of reaction is in part determined by the superior properties of these, it is sufficiently severe to prevent the less potent individuals from maintaining their numbers, and it becomes progressively more severe as displacement proceeds. Thus individuals of an original normal type (which could have persisted indefinitely had the new more potent type not appeared) are actively and completely eliminated by the increased environmental resistance induced by the appearance of the new type. There is a similar course of events if an environmental change gives an advantage to individuals which previously had no advantage.

Such compensatory reaction to changes in the properties of organisms is an essential complement of selection—for in its absence selection could not bring about replacement, which is a characteristic feature of evolution. Selection and the elimination of the less potent individuals by compensatory reaction proceed automatically whenever some individuals in a population have any inheritable advantage over others. It is not necessary for the operation of selection that the species should be in jeopardy; nor does the selection of properties which cause reduced mortality or increased fecundity necessarily lead to increased density for, as the experimental examples given here have shown, density may be changed but little or even decreased by properties greatly advantageous to the individual possessors. That is to say, selection operates upon individual differences without any reference to the success of the species; whereas density governed reaction compensates for even great changes in properties so produced and maintains populations in a stable condition in their environments before, during, and after selection.

These conclusions and their corollaries were reached and discussed in greater detail in an earlier publication (Nicholson 1927), and summarized by Nicholson (1933) and by Haldane (1949), who neatly epitomized the same arguments in a pair of dependent equations which he based upon the mathematical investigation of the interactions of insect hosts and their parasites made by Nicholson and Bailey (1935). The experiments briefly outlined here show that the essential underlying mechanism of compensation revealed in these earlier theoretical investigations is not restricted to host-parasite interaction; and, in particular, they demonstrate the actual existence of this mechanism.

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AN OUTLINE OF THE DYNAMICS OF ANIMAL POPULATIONS

By A. J. Nicholson*

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Contents

Summary 9

I. Introduction 11

II. Characteristics and classification of significant environmental factors 13

III. Some experimental evidence concerning population regulation 17

- (*a*) Intraspecific competition 17
- (*b*) Mechanism of balance 20
- (*c*) Automatic adjustment to external stresses 23
- (*d*) Complementary governing factors 27
- (*e*) General implications of experimental results 28

IV. Theoretical consideration of population regulation in simple situations 29

- (*a*) Populations at equilibrium 31
- (*b*) Population growth and maintenance in simple situations 33
  - (i) Density triggered reaction 35
  - (ii) Prompt density conditioned reaction 36
  - (iii) Tardy density conditioned reaction (contest) .. 40
  - (iv) Tardy density conditioned reaction (scramble) .. 42

V. Population regulation in complex situations 43

- (*a*) Climatic influences 43
- (*b*) Edaphic influences 46
- (*c*) Biotic influences 47
- (*d*) Population balance 50
- (*e*) Economic control of pests 51
- (*f*) Natural selection 52
- (*g*) Population dynamics 53

VI. Critical review of evidence and its interpretation 54

- (*a*) The place of thought in research 54
- (*b*) Critical review of some population theories 56
- (*c*) Basis and validity of conclusions in present investigation 58
- (*d*) Basis and validity of conclusions in earlier investigations by Nicholson and Bailey 61
- (*e*) The collection and interpretation of evidence: summary 63

VII. References 64

Summary

This article is itself a summarized statement concerning the various influences which affect population densities and the population systems these lead to. Known facts concerning animal populations have been analysed, systematized, and critically examined, using the experimental and mathematical

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approaches in the simpler situations. The more outstanding conclusions are listed below.

Populations are self-governing systems. They regulate their densities in relation to their own properties and those of their environments. This they do by depleting and impairing essential things to the threshold of favourability, or by maintaining reactive inimical factors, such as the attack of natural enemies, at the limit of tolerance.

The mechanism of density governance is almost always intraspecific competition, either amongst the animals for a critically important requisite, or amongst natural enemies for which the animals concerned are requisites.

Governing reaction induced by density change holds populations in a state of balance in their environments. The characteristic of balance is sustained and effective compensatory reaction which maintains populations in being in spite of even violent changes in the environment, and which adjusts their densities in general conformity with prevailing conditions.

Far from being a stationary state, balance is commonly a state of oscillation about the level of the equilibrium density which is for ever changing with environmental conditions.

Destructive factors do not add to mortality when they continue to operate over long periods, but merely cause a redistribution of mortality, for the intensity of competition automatically relaxes sufficiently to make room for the destruction they cause. Such compensatory reaction causes the effect of destructive factors upon density to be much less when balance is reattained than that which they produce when they first operate.

Although population densities can be governed only by factors which react to density change, factors which are uninfluenced by density may produce profound effects upon density. This they do by modifying the properties of the animals, or those of their environments, so influencing the level at which governing reaction adjusts population densities.

Population growth and maintenance are influenced in different ways by the four kinds of density governed reaction and the three kinds of governing requisites recognized, so giving rise to the twelve situations diagrammatically illustrated in Figure 6, and to the different patterns of population growth and maintenance characteristic of these.

Interaction between populations and their governing requisites often leads to oscillations in density even in a constant environment. Five kinds of population oscillations are recognized, namely, relaxation, coupled, lag, coupled-lag, anl fragmented oscillations.

Periodic environmental influences, such as the seasons, tend to impose their period upon oscillations of internal origin, and so to obscure their existence in spite of the fact that they may be dominantly responsible for the violence of the population changes observed.

Oscillations and fluctuations of the different populations in a community tend to interfere with one another, so giving rise to irregularities which may have no evident relation to varying external conditions.

Two or more species cannot be governed by the same factor, or group of factors, in the same place at the same time; but species with similar requirements may live together in some places, provided each has an advantage over all the others in some parts of the region they occupy.

Density governance is an important part of the mechanism of natural selection; for, as individuals with advantageous properties are selected, this causes an intensification of induced reaction which ultimately eliminates other individuals and their offspring which do not possess these advantages.

I. INTRODUCTION

Populations, like rivers, continue to exist only because new matter continually replaces the matter they inevitably lose. Flux is an inherent essential of their continued existence; and their distribution and size are functions of the rate of accession of suitable new matter, and of the local influences which determine how much of this they can take up. Population dynamics is the branch of biology concerned with the forces (that is to say, the measurable influences) which govern movement of matter through populations, from the environment and back again. Only by reaching an understanding of these forces can we expect to account for the distribution and densities, and for the changes in the distribution and densities, of populations which are observed in nature.

The primary force is solar energy, for all energy used by organisms, whether for the transport of matter or for other purposes, can be traced back to this source. The photosynthetic activity of plants traps some of this radiant energy, so enabling plants to build into themselves the inorganic materials from which the matter used by all organisms is ultimately derived. Photosynthesis, then, is the primary mechanism which makes available to organisms both the matter and the energy they use. Many different factors influence the way the matter is channelled through organisms, and from one organism to another, the energy expended in this process being obtained by the breakdown of organic materials, the products of which are ultimately excreted. Thus the energy originally trapped by photosynthetic processes is dissipated, and the matter originally elaborated by plants is returned to the inorganic environment as an inevitable result of metabolic processes. The matter remains available for re-use by organisms; but the energy is lost and has to be replaced by new solar radiation if life is to continue.

The forces which govern metabolism and reproduction, and also the forces which have governed the evolution of the innumerable kinds of organisms which exist, are clearly of fundamental importance in population dynamics; but we can regard these as the appropriate subjects of study in the separate, but closely related, sciences of the dynamics of individual organisms and the dynamics of evolution respectively. It is sufficient for the purposes of the present discourse to accept the fact that organisms have the properties we know them to possess, without specifically considering how these came into being, or the details of the metabolic processes which govern matter and energy exchange between individual organisms and their environments.

Animals not only build up and maintain their tissues by using organic food obtained directly or indirectly from plants, but they use some of it to produce offspring. This ability of organisms to multiply when conditions are favourable is of outstanding importance in all population problems, for it is the means by which populations can readily expand when the supply of the things they need increases. When this supply contracts, mortality tends to adjust the population to the new environmental conditions, for the death of some individuals permits the survivors to obtain more adequate quantities of these essentials. Thus reproduction and death are the properties of organisms which are ultimately responsible for the ability of populations to adjust their densities to the prevailing supply of the things needed.

Although it is true that the size of any population tends to vary directly with the amount of food the constituent individuals collectively use, it must not be assumed that food supply is the only thing which can limit population size. It often happens that populations are limited by other factors (such as natural enemies, or the availability of suitable space) at levels far below those which the food supply would permit. Moreover, as will be shown later, population densities do not necessarily vary in direct proportion to the amount of food the constituent individuals use, for some may be wasted in greater or lesser measure according to the circumstances.

Throughout the ages organisms have been continually producing adaptations which enable them to occupy previously vacant space—or to displace other kinds of organisms from the space, or parts of the space, these previously occupied. This has led on the one hand to the occupation of more and more of the earth's surface, and on the other to diversification of organisms. This expansion of the area occupied by plants has caused an increase in the amount of solar energy used, and so also of elaborated organic matter, which is potential food for animals. The diversification of plants by adaptation to different kinds of habitats has constituted a further diversification in the habitats available to animals. Adaptation to these new habitats, and to the new habitats phytophagous animals themselves constitute or create, has led to the further diversification of animals. Because of this diversity the energy and matter primarily obtained by plants is channelled through complexes of associated organisms which vary in composition greatly from place to place; and the forces which govern this channelling are those which, influenced by the properties of the various species, and those of their environments, determine the spatial distribution and densities of these species.

The analysis presented in the following pages of the factors and mechanisms which determine the distribution and densities of populations is given only in bare outline, for the field covered is enormous. The views put forward make some contact with almost everything that has been written about populations, and so comparison of these with the views expressed by other authors must, with few exceptions, be left to later more detailed publications dealing with particular aspects of the subject. This outline has been produced expressly for the purpose of providing a framework into which can be fitted more detailed articles concerning the experimental and theoretical investigations I have carried out over a number of years.

As many of the concepts outlined in the following discussion are either new, or differ in some respect from those used by other authors, it has unfortunately proved necessary to use new terms to represent them. For this purpose English words have been selected which can be used to convey the ideas intended without any departure from ordinary English usage. Their meanings conform to those given in the Shorter Oxford English Dictionary.

II. CHARACTERISTICS AND CLASSIFICATION OF SIGNIFICANT ENVIRONMENTAL FACTORS

It is axiomatic that organisms can live and multiply only when all their numerous essential requirements are satisfied. An environmental element or group of elements, which satisfies any one of these requirements is a *requisite.* Food and favourable living space are primary requisites for all organisms, but each can be subdivided into many distinct elements. In particular situations it may be convenient to recognize that food consists of various distinct requisites, such as protein, carbohydrates, salts of particular kinds, or other chemical constituents; or to specify the requisites as, for example, plants belonging to particular species, particular parts of those plants, or these parts when at a particular stage of development. With favourable space it may be necessary to specify separately such requisites as warmth and moisture (within known limits of tolerance), refuges, nesting sites, and suitable media in which to live. The degree to which essential things are grouped together or separated when defining requisites depends upon the needs of each particular investigation. For example, with a monophagous predator it is sufficient to define the food requisite as the prey species, without referring to the numerous chemical constituents which each play an essential part as food.

There is a quantitative or qualitative lower limit to the favourability of any requisite. When (even in the absence of competition by other individuals of the same species) this *threshold value* is not exceeded by any one requisite the population cannot persist, no matter how favourable any or all of the others may be. This happens, for example, if the right food is present but so sparse that individuals cannot obtain sufficient to maintain themselves and to produce offspring at the replacement rate; if temperature is below the limit of tolerance of the species under the prevailing conditions; or if the degree of freedom from attack by natural enemies is insufficient to permit survival of offspring at even the replacement rate. Clearly, therefore, the spatial distribution of any species is limited at all points at which the favourability of any one of its requisites falls below the threshold value under the prevailing conditions. It should be noted that the threshold value of a particular requisite for a given species is not a constant, for it varies somewhat with environmental conditions. For example, it is well known that with certain insects the limits of tolerable temperature vary markedly with the humidity conditions.

Within regions where all the requisites of a given species exceed their thresholds of favourability the species population not only can exist, but inevitably grows. However, sooner or later a check to continued population growth is inevitable, for the growing population progressively depletes such things as food and favourable space, and it may otherwise impair the favourability of the environment, as by the accumulation of harmful metabolites, or by inducing heavier attack by natural enemies. These effects of population growth reduce the favourability of the environment until it falls to the threshold value, when further growth is made impossible.

When considering the influence of requisites upon the distribution or densities of populations, it is generally necessary to specify the particular properties of the requisites which are important under the prevailing conditions. For example, the properties "density", "rate of generation", "quality", and "accessibility" of food all individually influence population survival and density. Properties of requisites, and also those of the animals themselves, which have discrete influences upon populations are here referred to as *density factors.* The limitation of spatial distribution which such factors exercise can be regarded as the imposition of extreme density limitation in the areas from which they exclude the animals. Inimical factors (such as adverse temperatures, or the density or activity of a particular natural enemy) are regarded as qualifying attributes of the requisite "favourable space". When animals or plants are attacked by natural enemies, they are themselves requisites, and their density or availability are factors which may influence the densities of their natural enemies.

When we are concerned with the immediate influence of the environment upon populations it is usually most convenient to regard this as explicable in terms of the effects produced by such density factors. On the other hand, when dealing with the longer range effects produced by the interaction between populations and their environments, it is necessary to specify the requisites of which the density factors are attributes, for (as will be shown later) the patterns of population change and maintenance are greatly influenced by other attributes of the requisites, such as their inherent qualities of transience, persistence, temporary existence, and multiplication.

In order to make clear the effects environmental factors may have upon populations, it is necessary to distinguish between several categories of requisites and factors. An *unresponsive requisite* or factor is one which remains unaltered in spite of any change in the population considered. For example, the prevailing climatic conditions are quite unaffected by any change in the densities of most kinds of animals. A *responsive requisite* or factor, on the other hand, is affected by change in population density, as when the increasing amount of food used by animals in a growing population causes a progressive reduction in the amount remaining unused at any moment. If the quantity or quality of the requisite is not only affected in this way by density change, but in turn modifies its influence upon population change, the requisite is *reactive.* It does not necessarily follow that an induced change in a requisite will change the influence of the requisite upon the population. For example, if the population is limited by the action of natural enemies at a level far below that permitted by the food supply, an increase in density produces a response in the food supply but no reaction by it; for, although population growth undoubtedly does cause greater depletion of food, this has no effect upon the population, food being still available to individuals in excess of requirements. Such responsive requisites, in common with all unresponsive requisites, are *non-reactive requisites.*

When population densities are far below the capacity of the environment it sometimes happens that population growth causes the properties of a requisite to become more favourable, so inducing still further growth. Influences which augment change in this way are *density disturbing factors.* For example, the trampling down of shrubs and old grass by herbivores in a sparsely occupied environment may increase the amount of palatable grass subsequently available to the population or, if the population is reduced below a certain critical density, trampling may be insufficient even to keep clear the then available amount of pasture, so that this decreases progressively with time. Invariably such augmentative reaction to density change is replaced by density governing reaction as the population approaches the capacity of the environment.

It is more usual for reaction to oppose change in density; for increase in population must sooner or later lead to significant reduction in the quantity, quality, or accessibility of one or more requisites, and this inevitably slows down growth and eventually precludes any further growth. The properties of requisites which react in this way are *density governing factors,* for it is their reaction to density change which holds population densities in relation to environmental conditions.

Non-reactive requisites, whether responsive or unresponsive, are incapable of bringing about such adjustment. For example, food which remains in excess, and favourable climatic conditions which remain unaltered by population growth clearly cannot check progressive growth. The quality of the food or the temperature prevailing, however, may have an important effect upon the level at which a population is adjusted by governing factors; for these factors may alter the properties of the animals (such as their activity, viability, and reproductive powers), or those of the governing requisites (such as the quality or rate of supply of food) and, as will shortly be shown, governing reaction adjusts population densities in relation to such properties. It may be said, then, that non-reactive factors may play a part in laying down the rules which are enforced by the governing factors, such non-reactive factors being referred to as *purely density legislative.* It should be noted that density governing factors are also density legislative, for it is the amount and quality of the governing requisite which determine the size of the population which can be borne under the prevailing conditions when limiting depletion is reached.

In brief, governing factors are the primary determinants of population densities, both in their governing and their legislative capacities; whereas non-reactive factors modify these densities by influencing the properties of the animals, and also those of the governing factors. Thus, as governing and legislative factors together determine population densities, they may be referred to collectively as *density regulating factors,* for the verb “to regulate” commonly has the two component meanings of rule making and rule enforcement —although it sometimes signifies rule making only.

The interrelationship of these density factors which are properties of requisites is shown diagrammatically in Figure 1. One factor shown there has not been discussed, as it is not strictly speaking a density factor. A *density inactive factor* is a property of a requisite which does not affect density, although it is essential for the existence of animals. Thus the supply of sea-water does not influence the number of marine animals which can live in unit volume, but there must be such a supply if the animals are to exist, and its extent places an extreme limit upon their possible distribution. Similarly, the supply of oxygen for terrestrial animals commonly does not vary significantly, and so, although absolutely essential for most animals, it does not influence their densities.

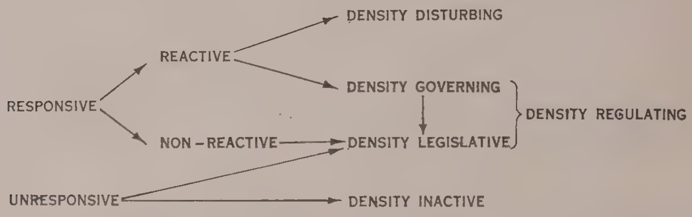

Fig. 1.—Classification of requisites and of their properties in relation to their response to density change and to the influence they have upon population density.

It sometimes happens that factors which do not themselves respond to density change act as the tools or *instruments of destruction* used by true reactive factors. Thus increasing density, instead of causing increasing mortality or decreasing natality in such ways as the depletion of the food supply or of the amount of favourable space still unoccupied, may cause a greater proportion of the animals to move into parts of the environment intrinsically less favourable than those they would occupy by preference. Clearly the underlying mechanism of this increasing exposure to destructive influences is competition for food or favourable places; but the immediate cause of destruction may be unfavourable temperature, or attack by general predators which could not reach the animals in their preferred habitat. In such situations it is confusing to speak of such destructive agencies as "density dependent factors", as has been done by several authors (see Solomon 1949) when arguing that climatic factors may directly control population densities. Clearly the "density dependent factor" is the availability of food or favoured places, whereas the adverse climatic factors merely destroy such individuals as the dispersive effects of competition expose to their influence.

It has long been realized by many biologists that the observed general relation between population densities and environmental conditions could only be brought about by reactive factors which permit populations to grow when at relatively low densities, and oppose growth when the densities become relatively high. Various terms have been proposed for such reactive factors, the one in general use in recent years being *density dependent factor*. This appears to have given rise to some confusion, for it implies any significant environmental element or quality which is influenced by density, and thus might be taken to have the meaning given the term "density responsive factor" here. The term is often used in this loose sense; so, to avoid misunderstanding, it is necessary to replace it by a term which signifies the characteristic effect of such factors upon density, rather than the effect of density upon them (which is an attribute of other kinds of factors as well). "Controlling factor" (Nicholson 1927, 1933) conveys the correct idea, but unfortunately may lead to confusion when discussing population problems related to the control of pests, for in this context "to control" has the meaning "to modify the control so that the density of the pest is reduced to a point at which the economic damage caused is negligible" (Nicholson 1933). The term "density governing factor" has therefore been substituted, but its meaning is precisely that of "density dependent factor" according to definition (Smith 1935).

"Density independent factor" is still less apt, for its significant characteristic is not that it is uninfluenced by density but that, even though it may respond to density change, its effect upon density remains unaltered. "Non-reactive factor" has therefore been substituted, this term including both unresponsive and non-reactive responsive factors.

III. Some Experimental Evidence Concerning Population Regulation

It is easiest to appreciate how populations accommodate themselves to the varying conditions of their environments by examining what happens to populations of a given species when maintained under widely differing experimental conditions.

(*a*) *Intraspecific Competition*

The experiments upon which Figure 2 is based were briefly described in a previous article (Nicholson 1948) as follows:

"A number of glass tubes, each containing one gramme of homogenized bullock's brain as food, were used, and in each of these a different number of freshly hatched *L. cuprina* larvae was placed. Such series of cultures were replicated many times. The number of emerging adults was then plotted against the number of larvae from which they had been derived. It was found that with progressively increasing densities of larvae, mortality at first increased only slowly, but the size of pupae and of adults fell progressively. However, this kind of compensation for increasing competition for food cannot continue indefinitely. A point was soon reached beyond which mortality increased rapidly with larval density and the number of adults produced per gramme of medium fell progressively with further increase in larval density.

"These relations are shown clearly in the accompanying figure. In this particular example, eggs laid at intervals of two hours over an eight-hour period were used, each of the five batches of eggs contributing equally to the numbers of larvae used in any one culture tube. A curve with the same general characteristics was obtained when there was no appreciable age distribution, all the eggs being laid within a period of one hour, the only important difference being that the descending part of the curve was much steeper."

These experiments demonstrated the important part played by the wide scatter in the properties of animals upon the reaction of populations to depletion of their requisites. Examination of the cultures showed that even when no individuals were given special advantages there were very great differences in the rates at which the individuals grew, so that when the food was exhausted some individuals were comparatively large and some small. These differences were accentuated when (as in Fig. 2) some individuals were given the special advantage of having access to the food earlier than others. The result of this was that the number of larvae reaching a sufficient size to produce viable pupae when the food was exhausted fell progressively with larval density. Were there no such scatter of properties and opportunities, increasing density would produce no mortality until the point was passed at which the amount of food obtained by each individual fell below that necessary for the production of viable pupae; at this and all higher densities there would be no survival.

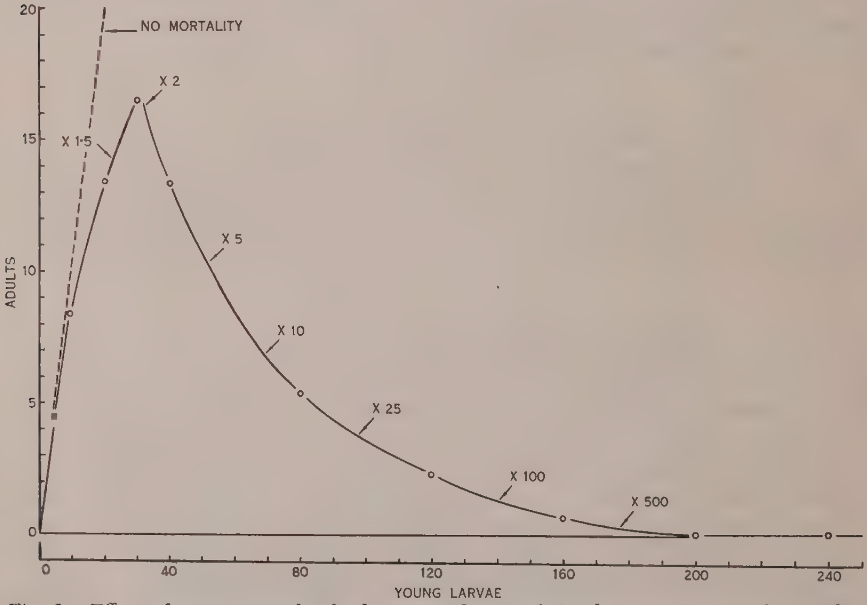

Fig. 2.—Effect of competition for food amongst larvae of *Lucilia cuprina* upon the number of adults produced (see text).

Figure 2 shows that, above a certain critical density, further increase in larval density causes not only an increase in the percentage mortality but also an actual reduction in the number of adults produced from the gramme of food consumed. This is because increasing quantities of food are consumed by the increasing number of larvae which fail to mature. Starting at a low density, then, the tendency is for a population to grow progressively so long as a surplus of offspring survives. Further growth is rendered impossible when the percentage of offspring destroyed by competition equals the percentage which is surplus to that necessary for the replacement of mature animals as they die. Consequently, the greater the power of increase (i.e. the ratio of offspring to parents in the absence of competition effects) the smaller is the number of adults produced from a given quantity of food at equilibrium. This is clearly shown in Figure 2, in which the points indicated by numbers preceded by the multiplication sign show the equilibrium levels of larvae and adults at each power of increase represented by these numbers. Inspection shows that any departure of density from the equilibrium level for any given power of increase (which is assumed to remain constant) leads to an oscillation about this level; unless the power of increase is less than 2 (in the example given), when an asymptotic approach to this level results (see Nicholson 1948).

However, whether the population oscillates or not, the reactive influence of competition causes populations to be adjusted at or about the levels represented by their equilibrium densities. Consequently, if some adverse environmental factor causes a reduction of the birth-rate or the destruction of some of the surplus offspring produced, this lowers the power of increase of the animals and so increases the number of adults produced.

The important part played by the wide scatter of the properties of animals and those of their environments in population dynamics cannot be overemphasized. On the one hand it permits populations to adjust themselves to their changing environments in the way just described, and so strongly influences both densities and patterns of population change; and on the other it permits populations to persist under conditions far more adverse than could be withstood if all individuals had only the average properties and opportunities, and if no parts of the environment were more tolerable than others. The greater the surplus of offspring produced, and the wider the scatter of the properties and opportunities of the individuals, the greater is the ability of the population to accommodate itself to adverse conditions.

Experiments such as that graphically represented in Figure 2 illustrate the fact that when any requisite is in short supply, the individual animals get as much of it as they can, and so reduce the amount available to other individuals. It is this reactive lessening of the favourability of the environment which prevents the indefinite growth of populations, and holds population densities in general relation to the prevailing conditions. This state of reciprocal interference which occurs when animals having similar needs live together and which influences their success is here called *competition*. This use of the term has been criticized (e.g. Dobzhansky 1950) on the ground that the word "competition" has an emotional content and implies the taking of active steps against competitors. In this restricted sense the word would be applicable only to the actions of some of the higher animals; but such restriction of meaning is unwarranted, as it commonly does not apply in ordinary usage. For example, in art competitions the competitors are not expected to take action directly against one another—each simply paints as well as he can and the prize goes to the one who does best. The derivation of competition (*com*: together; *petere*: to seek) also indicates its appropriateness in the present context. It should also be noted that the sense in which "competition" is used here conforms exactly with normal usage in plant ecology.

It is necessary to distinguish between two kinds of competition, as they produce different effects upon the patterns of population growth and maintenance. *Scramble* is the kind of competition exhibited by a crowd of boys striving to secure broadcast sweets, and is illustrated by the competition of *L.*

cuprina larvae already described. Its characteristic is that success is commonly incomplete, so that some, and at times all, of the requisite secured by the competing animals takes no part in sustaining the population, being dissipated by individuals which obtain insufficient for survival. With *contest,* on the other hand, the individuals may be said to compete for prizes (such as a host individual, or an amount of favourable space an individual can arrogate to itself) which each provides as much of the requisite as an individual needs to enable it to reach maturity, or provides fully for the development of one or more of its offspring. Thus the individuals are either fully successful, or unsuccessful; and the whole amount of the requisite obtained collectively by the animals is used effectively and without wastage in maintaining the population.

(*b*) *Mechanism of Balance*

The foregoing considerations, and the experiments they are based upon, show how competition may be expected to influence populations. In order to test the conclusions reached many cultures of the Australian sheep blowfly, *Lucilia cuprina* Wied., have been maintained, each under a different set of conditions. The essential feature of such cultures is that the populations are left to develop and maintain themselves without interference—the only action taken, apart from keeping daily records, being the maintenance of the conditions decided upon at the beginning of the experiment, including the provision of a continuous supply of those requisites the insects expend. Only brief reference can be made here to some of these experiments.

Figure 3 illustrates the population changes which took place in a population maintained under as nearly constant conditions as possible. The culture room was held at 25°C, water and sugar for the adults, and also larval food (to which the adults did not have access), being provided in excess of requirements at all times. The governing requisite was ground liver, which was available to the adults alone, and each day 0.5 g of this was placed in the breeding cage. In common with the other experiments referred to in graphs and tables here, the initial parts of the culture are not recorded in Figure 3 because they are not pertinent to the present discussion.

The outstanding characteristic of this culture was the maintenance of violent and fairly regular oscillation in the density of the adult population. The reason for this is simple. It will be observed that significant egg generation occurred only when the adult population was very low. At higher densities competition amongst the adults for the ground liver was so severe that few or no individuals secured sufficient to enable them to develop eggs. Normal mortality, therefore, caused the population to dwindle until the consequent reduced severity of competition permitted some individuals to secure adequate liver and so to lay eggs. As it takes more than 2 weeks for the eggs so generated to give rise to new adults, the population continued to dwindle for this period, during which many more eggs were generated, for competition amongst the adults for ground liver continued to slacken. The eggs then generated in due time gave rise to new adults, which led to a rapid increase in the adult population, and the resultant overcrowding caused virtual cessation of egg production. A new cycle of oscillation then began.

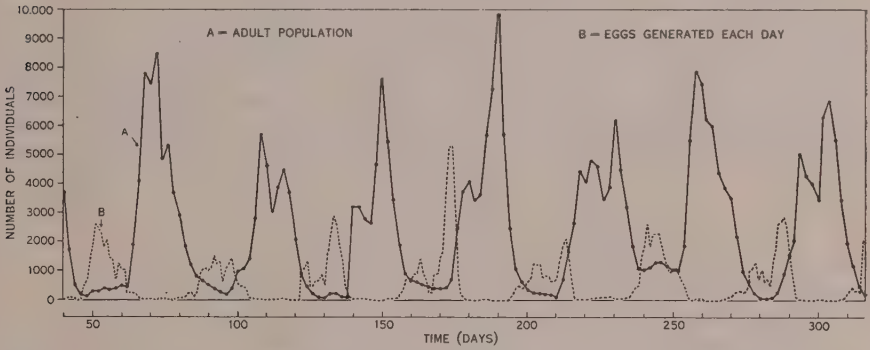

Fig. 3.—A population of *Lucilia cuprina* governed by the daily supply of 0.5 g of ground liver for the adults. *A* is the observed adult population; and in *B* the number of eggs generated each day is plotted at times 2 days before they were actually laid, this being the time taken in development after the intake of adequate food. (The lack of a clear inverse relation between the various low adult densities and the number of eggs produced is due to the fact that adults are mostly senile as the adult minima are approached, near the minima many are newly emerged and incapable of laying eggs, and subsequently highly fertile young individuals dominate.)

If increased acquisition of food were to cause fully mature adults to come into being immediately (instead of merely initiating the subsequent production of eggs and the still later development of adults) this prompt reaction would cause the system to be non-oscillatory. This is because reaction would cause the population first to approach, and then to maintain the *equilibrium density* of the species under the prevailing conditions, this being the density at which production of offspring precisely compensates for the loss of adults by death; for any departure from this level would immediately bring compensating reaction into play, and this would cease as soon as the equilibrium density was attained again. This, then, is the balancing mechanism which holds population density in general relation to the prevailing conditions; and the system of balance is often highly oscillatory, simply because animals commonly take a significant time to grow up, so causing a time lag between stimulus and reaction. During this lag period the stimulus continues to generate more and more reaction, and this continues to come into operation for a similar lag period after reaction has removed the stimulus.

If such violent oscillation as is shown in Figure 3 were observed in nature, one might well conclude either that there must be some periodic element in the environment underlying it or, alternatively (as the maxima are some hundreds of times as great as the minima) that population density is unrelated to the constant environmental conditions. However, not only do we know that there was no external periodic influence under the conditions of culture, but also we have observed in detail the mechanism which causes the oscillation. As to the suspicion that the general density level has no relation to the environment, this is shown to be untrue by comparison with other experiments. The culture illustrated by Figure 3 was supplied with 0.5 g of ground liver per day and the average density of adults was found to be 2520. In another culture in which all conditions were precisely the same, except that only 0.1 g of liver was provided per day for the adults, the average density of adults was 527. Thus, in spite of the violence of the oscillations produced in both cultures, the average density was almost precisely proportional to the supply of the governing requisite.

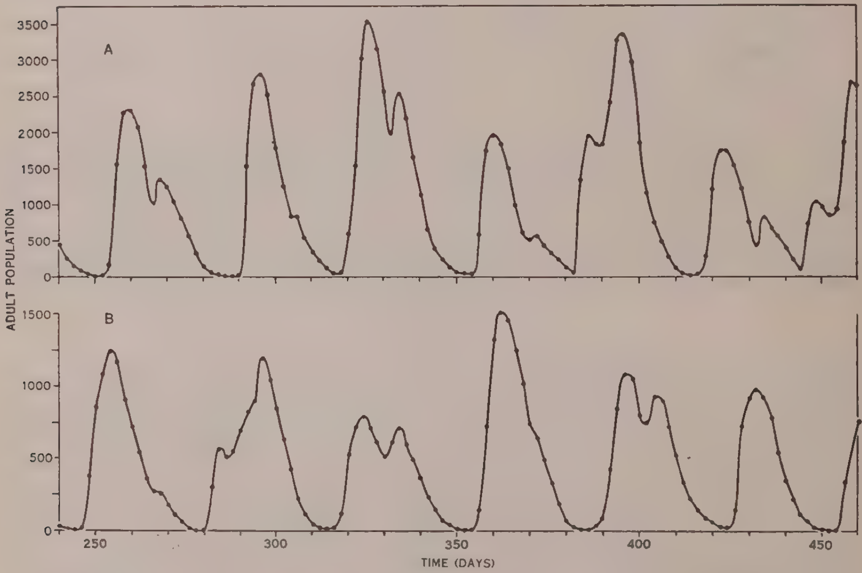

Fig. 4.—Adult populations of *Lucilia cuprina* governed by the supply of meat for the larvae—excess ground liver, water, and sugar being supplied for the adults. In *A* 50 g of larval food, and in *B* only 25 g, was supplied. Note that the vertical scale in *A* is only half that in *B*.

This point is further illustrated by Figure 4, but in these cultures (which were run concurrently), the adults always had excess ground liver available, whereas the daily supply of larval food was restricted to 50 g of meat in *A* and 25 g in *B*. To simplify comparison *B* has been drawn to double the vertical scale used in *A*. It will be seen that the form, violence, and period of the oscillations in the two cultures are essentially the same, and that the average density of *B* is approximately half that of *A*; that is to say, the average densities are proportional to the supply of larval food, which is the governing requisite.

These examples illustrate what is meant by the balance of populations (see Nicholson 1933). Some biologists have expressed the opinion that the term is inappropriate (e.g. Solomon 1949), but this appears to be due to an unjustified belief that "balance" and "equilibrium" are synonymous. The ordinary usage of the word "balance" implies controlled movement, or at least potential movement, about a position of true equilibrium. Think, for instance, about the balancing feats one sees on the stage or at a circus: always the mechanism is expertly controlled corrective movement which opposes each departure from the position of equilibrium. *Balance* refers to the state of a system capable of effective compensatory reaction to the disturbing forces which operate upon it, such reaction maintaining the system in being. It is the exceedingly important state of compensatory reaction upon which populations, in common with ships on stormy seas, depend for their continued existence.

(*c*) *Automatic Adjustment to External Stresses*

Not only can governing reaction hold populations in a state of balance at levels associated with the supply of a requisite, such as food, but within very wide limits it can adjust populations to withstand the effects of adverse environmental factors. Many experimental examples of this have been given elsewhere (Nicholson 1954). To illustrate the mechanism of compensation some details are given in Tables 1 and 2 of another pair of cultures. In these 50 g of meat were placed in each culture every day, both larvae and adults being dependent upon this. Thus the culture conditions were essentially the same as in the experiment described elsewhere (Nicholson 1950), the oscillations in *A* being similar to those there illustrated. In *A* there was no imposed destruction, whereas in *B* 50 per cent. of all adults present in the cage were destroyed every second day by bisecting the interior of the cage with a guillotine-like partition, and allowing the adults in one half of the cage to die. It will be seen that this resulted in the destruction of 79 per cent. (100 × 337/426) of all adults produced (this exceeds 50 per cent. because many adults were exposed to destruction several times). However, not only was there this great destruction, but the age composition of adults was greatly altered—the population naturally consisting dominantly of young individuals. So, as adults do not begin to lay eggs until they are at least 2 days old, this destruction greatly reduced the mean birth-rate, in addition to shortening the mean adult life span (Table 2), and both these factors contributed to the reduction of the coefficient of fertility (that is, the number of offspring produced on the average by an individual during its lifetime, both males and females being included when calculating the average, just as with birth-rates). In spite of this great destruction of adults and reduction of fertility, the average population of adults was virtually the same in *B* as in *A*, in which there was no imposed destruction (Table 1).

Actually this reduction of the coefficient of fertility in *B* was part of the compensation for imposed destruction, for more adults had to exist in order to produce sufficient eggs to cause any given degree of larval competition. In addition, columns *a* and *b* in Table 1 show that further compensation was due to an increased rate of production of adults in *B* from the smaller number of eggs laid, compared with *A*. This clearly was due to lessened larval competition, the mechanism being that illustrated in Figure 2.

TABLE 1

AVERAGES OF OBSERVED QUANTITIES IN TWO CULTURES OF *LUCILIA CUPRINA*, IN WHICH THE POPULATIONS WERE GOVERNED BY THE COMPETITION OF BOTH LARVAE AND ADULTS FOR 50 g OF MEAT SUPPLIED DAILY OVER PERIODS EXCEEDING 7 MONTHS

Situation	Larvae Hatched per Day *a*	Adults Emerged per Day *b*	Adults Destroyed per Day *c*	Natural Deaths of Adults per Day *d*	Mean Adult Population *e*
A—No imposed destruction	4287	220	0	220	1498
B—50% adults destroyed every second day	2248	426	337	88	1456

In all environments tolerable to a population, the position is automatically reached at which the number of individuals dying, whether from natural causes or imposed destruction, in any long period equals the number produced in the same period. That this actually happens is shown by the data in Table 1 (columns *b*, *c*, and *d*), and also in the tables given elsewhere (Nicholson 1954) concerning many populations of *L. cuprina* subject to greatly varying conditions, including heavy destruction and conditions which seriously affect birth-rate. The agreement between recorded average figures for natality and mortality is always very close. This at first sight seems surprising, having observed in many populations the violence of the oscillations which have their origin in great inequalities of natality and mortality; but it follows from first principles

TABLE 2

CHARACTERISTICS OF THE POPULATIONS DERIVED FROM THE DATA IN TABLE 1, USING THE EQUATIONS AT THE TOP OF THE COLUMNS

Situation	Total Mortality Due to			Mean Adult Life Span	Mean Birth-rate	Mean Coefficient of Fertility
	Larval Competition $f=\frac{100(a-b)}{a}$	Imposed Destruction $g=\frac{100c}{a}$	Natural Deaths of Adults $h=\frac{100d}{a}$	$i=e/b$	$j=a/e$	$k=a/b=ij$
A	94·9%	0	5·1%	6·8	2·9	19·5
B	81·5%	14·7%	3·8%	3·4	1·6	5·4

that such agreement must exist in any population which neither increases nor decreases its general level over long periods.

It is evident from these considerations that imposed destruction (within the limits of tolerance of a population) does not add to mortality, except as an immediate and transient effect; for mortality due to reactive factors is correspondingly and automatically reduced until only the surplus of offspring is destroyed, just as it was before the new destructive factor operated. Thus Table 2 shows that the imposed destruction of 79 per cent. of adults led to a readjustment of mortality distribution such that this destruction became 14.7 per cent. of all individuals—place being made for this by a reduction of 13.4 per cent. in the mortality due to larval competition for food, and of 1.3 per cent. in that due to senility (see columns *f* and *h*, Table 2). The key effect of destruction in this example was the reduction of the birth-rate, due to the changed age composition of the adult population. Because of this the adult population in *B*, although approximately equal to that in *A*, produced only about half the number of eggs per day, so lessening larval competition and leading to a daily emergence of about twice as many adults as were produced in *A*. Although 79 per cent. of these were destroyed sooner or later by the imposed factor, they all contributed for a time to the adult population recorded; but this was not double that in *A* simply because the average life span of the individuals was reduced to half. In this example, then, compensation for destruction was partly due to a reactive change in fertility, and partly to reactive change in the intensity of competition which led to a modification of the mortality distribution (see Table 2), the total mortality remaining at 100 per cent., just as it was without any imposed destruction.

In the cultures (Nicholson 1954) in which different percentages of adults were destroyed at emergence, the imposed destruction naturally did not have any direct effect upon the age composition of the adult population. In cultures in which populations were limited by larval food, therefore, the necessary compensatory reduction of larval competition could only be produced by a reduction of the adult population, for the reproductive rate was independent of density, the adults always having excess food available. This is what happened, but it was found that the reduction of the adult population was far less than the percentage of imposed destruction—the destruction of 99 per cent. of the emerging adults, for example, causing a reduction of the average adult population to about one-tenth, instead of to one-hundredth, of the population free from imposed destruction. This was because the lessened larval competition (due to the reduction of the adult population, and so also of the number of eggs laid) caused far more individuals to reach the pupal stage, as is strikingly illustrated by Figure 5.

On the other hand, in another series of cultures (identical to the foregoing except that adult food, instead of larval food, was the governing requisite) compensation was produced wholly by reactive changes in fertility. Without imposed destruction, adult competition for the limited supply of ground liver adjusted the fertility coefficient at 1.1. The coefficient of fertility was not unity in this instance simply because there was a mortality, due to unknown causes, of about 8 per cent. amongst developing individuals, which was apparently independent of density. With increasing percentages of destruction of the emerging adults, this coefficient increased correspondingly, being, for example, 10.8 with 90 per cent. destruction. Such compensation is due to the fact that destruction reduces the number of adults surviving and so lessens the competition amongst them. Consequently, as the adults individually obtain more ground liver, on the average, than before, they lay more eggs; and governing reaction causes the adult population always to tend towards the level at which just sufficient surplus eggs are laid to compensate for the imposed destruction. As in the previous examples, the reduction of the population was not proportional to imposed destruction—90 per cent. destruction, for example, only reducing the adult population to about one-third.

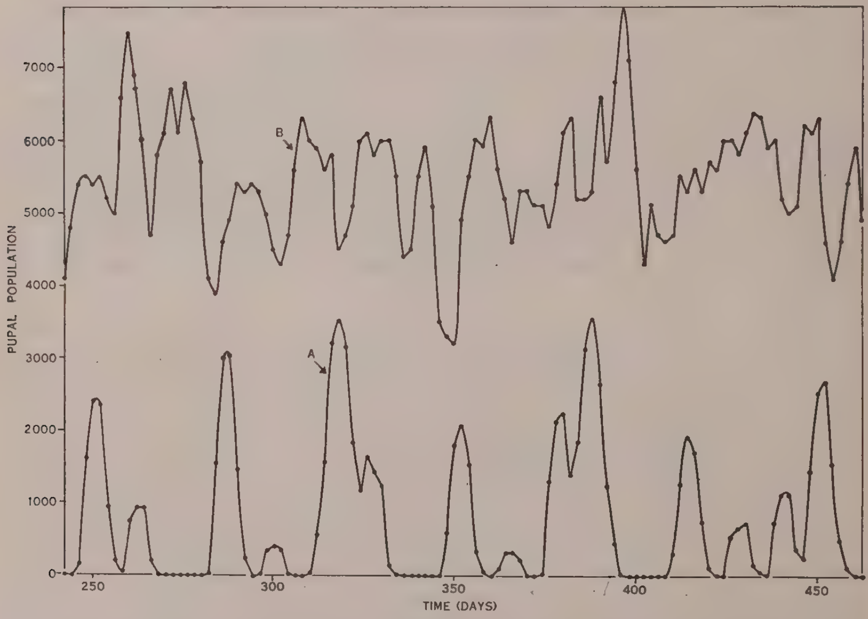

Fig. 5.—*A*, the population of viable pupae in the same *L. cuprina* culture as *A* in Figure 4; *B*, the population of viable pupae in a concurrent culture similar in all respects to *A* except that 99 per cent. of the adults emerging each day were destroyed.

The foregoing examples show that populations can adjust themselves to even very heavy destruction, and that such destruction induces reaction which always tends to counter its direct effects. This it does by increasing the density of the age-group immediately preceding the one subject to destruction, and this in turn induces further reactions which either increase or decrease the densities of other age-groups, according to the circumstances. This is in conformity with conclusions reached elsewhere (Nicholson 1933, C.9* and C.18; Nicholson and Bailey 1935, C.16, C.17, C.18, C.31, and C.32) concerning the effect of introducing a new destructive factor (possibly another species of parasite) when the density of the host species is governed by specific parasites.

Populations not only adjust themselves to destructive factors, but also to any other change in the favourability of the environment—provided this does not exceed the generally very wide limits of tolerance of the species. Thus in a series of cultures governed by larval food supply, the average life span of the adults was made different by supplying each culture with an excess of a sugar solution at a concentration differing from those of the solutions used in the others. Sugar has an important effect upon the longevity of adults (at least in crowded cultures) and the sugar intake of the adults was limited by their capacity to take up liquid. The life span was found to decrease markedly with reduction in the concentration of the solutions. The effects were similar to those produced when the adult life span was shortened by direct destruction (see Table 1)—the adult population increasing a little, and the rate of emergence of adults increasing considerably, as the sugar content of the solutions and the life span of the adults decreased.

In another experiment, in which larval food was the governing requisite, the adults were given a poor oviposition site. This reduced the birth-rate to about one-third, and the consequent reduction of larval competition raised the adult population to 1667, compared with 1252 in an otherwise similar culture in which the oviposition site was good.

(*d*) *Complementary Governing Factors*

When new responsive factors are introduced they strongly tend either to displace the original governing factors, reducing these to the status of purely legislative factors, or to operate themselves as purely legislative factors. The new and old responsive factors can operate together as *complementary governing factors* only if each produces a significant effect upon the population when responding to the same density change. That is to say, both factors must react significantly to a similar range of densities.

This is very clearly illustrated by the series of population experiments with *L. cuprina* already referred to. The readily controllable variables were the supply of food for the larvae, and of ground liver, water, and sugar for the adults. In most of the experiments one of these depletable materials was selected as the governing requisite, and it was supplied at a constant rate sufficient to maintain a population within the capacity of the breeding cage. The others were supplied in excess of the requirements of the insects at all times, and so were purely legislative factors; for, although most noticeably responsive to density, the variation in the amount remaining unused had no significant effect upon the competing individuals, being always in excess of requirements.

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* The words "lower" and "higher" are incorrectly placed in Conclusion 9, as the arguments accompanying it show. C.9 should read "According to whether a destructive environmental factor operates before, after, or at the same time as a given parasite species, both the initial and final steady densities of the host species are respectively higher than, lower than, or the same as they would be if the parasites were alone responsible for destroying the surplus hosts."

In a few experiments the supply of each of two of these requisites was so adjusted to that of the other that there was significant depletion of both at the same general level of population, and so each played a governing role. For example, as it appeared that at the average density of a population governed by a daily supply of 50 g of larval food the adults needed only about 0.5 g of sugar, only this quantity of sugar was supplied per day, ground liver and water being maintained in excess—whereas all three adult requisites were in excess in the control culture. The experimental and control cultures were each supplied with 50 g of larval food per day. The average population level was very little affected by the reduction in the sugar supply, but reaction was more efficient, for the peaks of the oscillations were greatly reduced owing to the much shortened life span of the adults (due to sugar deficiency) when the population exceeded the average level. In another example (Nicholson 1954) the daily supply of ground liver for the adults was limited to 1 g, sugar and water being provided in excess, and the larval food was supplied at 50 g per day. The consequent great increase in adult competition and the resultant great reduction in oviposition (and so also in larval competition) increased the average adult population to 4042, compared with 1252 in an otherwise similar culture in which unlimited ground liver was supplied to the adults.

In another experiment new density governing destruction was imposed by destroying all but five of the emerging individuals each day—which naturally means that the percentage destroyed increased with density. Although this reduced the adult population from 1252 to 63, it increased the daily emergence of adults from 157 to 774. This evidently approaches a limiting situation, however, for only 33.7 per cent. of the pre-imaginal individuals died, and there is reason to believe that the coefficient of fertility, which proved to be 233.5, is near the extreme capacity of *L. cuprina.* That is to say, competition was reduced to very low levels in both the larval and adult populations. Therefore, if the permitted emergence of flies were reduced further, there could be little compensatory reaction; and so the population size of all age-groups would then tend to be directly proportional to the number of flies permitted to emerge. This shows how a new reactive factor may completely take over governing functions from another.

(*e*) *General Implications of Experimental Results*

It is thus seen that whenever a population is subjected to adverse factors which either increase the chance of destruction of the animals or interfere with their production of offspring, reaction causes a relaxation of the intensity of competition and by so doing it compensates for the disturbing effects of such factors. When the governing requisite is food such relaxation of competition reduces the wastage of matter taken up by the population; for with adults a greater proportion is used for the production of offspring, and with larvae less is used up by larvae which obtain quantities inadequate to enable them to reach maturity. Population density is therefore not simply a function of the available amount of food, or even of the amount of food some other kind of governing factor permits the population to use, but is markedly influenced by the wastage of food commonly caused by competition; and it is competition for some limiting depletable requisite which regulates density by determining how much food a population is permitted to use and how much of this it wastes.

In brief, governing reaction does not merely operate to oppose any departures of a population from its equilibrium density, but also enables populations to adjust themselves to withstand very great environmental stresses (particularly when their inherent reproductive capacity is high), and to maintain themselves in a state of balance under widely different environmental conditions. Moreover, the reduction in density which adverse factors produce as a primary effect is always opposed by compensatory reaction, being lessened, or even converted into an increase in density, when the population adjusts itself to the continued operation of the adverse factor.

IV. THEORETICAL CONSIDERATION OF POPULATION REGULATION IN SIMPLE SITUATIONS

It has now been shown that populations of one particular type, exemplified by those of *L. cuprina,* both react to the environment and cause reactions in the environment in such a way that their densities are automatically adjusted in relation to the prevailing conditions. As will shortly be shown, however, there are many other kinds of population systems; so, very briefly, we will consider their known characteristics in order to determine whether populations of other kinds can also reach a state of balance with their environments. But first it is necessary to define certain important properties of animals and of their environments which have an important bearing upon this problem.

An individual animal clearly has only a limited field of action. The size of this is determined partly by properties of the species and partly by properties of the particular requisite concerned—such properties as the rate of movement of the animals, the distance at which they can perceive the presence of the requisite, their efficiency in obtaining this requisite when perceived, the conspicuousness or concealment of the requisite, protective qualities which oppose destruction by the animals, and movement of the requisite sought which influences the likelihood of contact with, or escape from, the animals. The joint effects of such properties upon the efficiency of animals in obtaining a particular requisite can be allowed for by defining the *procurement field* of the species, for the given requisite under the given conditions, as the maximum amount of space an average individual can exhaust of the given requisite in unit time when there are no new accessions of the requisite to the environment. When, as is generally assumed in the following discussions, the requisite is generated continuously, exhaustion clearly does not occur; but, when stimulated to their maximum efforts by scarcity of the requisite, the animals explore their procurement fields effectively, either by moving about or reaching out to obtain the requisite or, alternatively, by making use of movement which brings particles of the requisite into their ambit. Thus the procurement field is a measure of the maximum effective field of action of an average individual in a unit of time, and so of the intrinsic efficiency of animals in satisfying a particular need under prevailing conditions. The "area of discovery" (Nicholson 1933; Nicholson and Bailey 1935) of an entomophagous parasite is its procurement field measured as the area effectively explored by an individual during its lifetime.

For the existence of a species it is clearly necessary that there should be a sufficient quantity of each requisite in the space of the appropriate procurement field to supply at least the minimum needs of an individual. This minimum tolerable quantity is the *maintenance quantum* of the given requisite for the species living under the prevailing conditions. When this quantity is available to an average individual, it is just sufficient to maintain the individuals and permit them to produce sufficient offspring to replace those that die. It is influenced, not only by the needs of the animals and the qualities of the given requisite, but also by the abundance and qualities of the other requisites present. This is because the use of these requisites may influence the metabolic processes of the animals and so alter the amount of the given requisite needed. Although its value is so influenced, the maintenance quantum is an important requirement of individuals of a given species which can be specified quantitatively under any given set of conditions.

It should be noted that the word "quantum" is here used in its ordinary sense of "required or desired or allowed amount; as much as suffices" (O.E.D.). The idea of invariability associated with this word by physicists must not be transferred to the word in its present context. On the contrary, it must be recognized not only that its value varies with environmental conditions, but also that its value represents an average of the varied amounts of the given requisite obtained by different individuals in unit time when living under equilibrium conditions.

Requisites of a species which are continuously generated do not accumulate indefinitely in the absence of this species; for accumulation is always opposed by a process of attrition, due to such things as the action of other animals, deterioration caused by physical factors, or decay. Accumulation is arrested when the intensity of attrition counterbalances that of generation. If this limited accumulation of a requisite is such that there is less than the maintenance quantum in the procurement field of the given species, this species clearly cannot maintain itself in the given environment; but if it is such that there is exactly the maintenance quantum in the space of the procurement field, the species is just barely able to exist at an indefinitely low density—for any higher density would augment the attrition, so reducing the amount in a procurement field below the maintenance quantum. This minimum density of the requisite which will permit a species to persist is the *threshold density* of the given requisite for the species under prevailing conditions.

If accumulation of a requisite in the absence of the given species exceeds the threshold density, the introduction of this species will be followed by population growth, for the animals at first obtain more than their maintenance quanta. By so doing they deplete the requisite until, when it reaches the threshold density, further growth becomes impossible, provided that reaction takes effect immediately. But if, as commonly happens, there is some delay before reaction affects the population, growth continues for a time, so reducing the requisite below its threshold density, and this in turn inevitably causes a subsequent decrease in the population, as has already been shown in the experiments with *L. cuprina.* Thus reaction causes the requisite and the population to approach, or to oscillate about, their respective *equilibrium densities*—that of the requisite being the threshold density under the prevailing conditions, and that of the population being the density at which the animals use the requisite at the rate it becomes available.

For convenience in the discussion which follows of relatively simple situations, it will be assumed that some property of only one requisite functions as a governing factor in each. This seems likely to be generally true, for, as the rate of production of each requisite is commonly purely a property of the environment, it is improbable that two or more requisites should be produced by chance at such relative rates that they are depleted to near their threshold densities by the same density of animals. So, at equilibrium, all requisites are likely to remain in excess, except the one which is first reduced to its threshold density by a growing population; for no matter how abundant the other requisites may remain, the limiting effect of this one requisite prevents the maintenance of any higher density.

(*a*) *Populations at Equilibrium*

Initially attention will be confined to populations which consist of individuals which all have the same requirements and live in constant environments —the offspring, and also the governing requisite, being generated continuously at a constant rate. That is to say, we shall confine attention to very simple animals, such as certain protozoa which do not change their properties as they grow, and, when more complex animals are considered, we shall make the reasonable assumption that the governing factor affects only one developmental stage or age-group, such as the larvae, or the adults.

For equilibrium of the animals, an average individual must obtain its maintenance quantum of the governing requisite in unit time. This is possible only if the equilibrium density (G_E) of the governing requisite is such that there is one maintenance quantum (q) in the procurement field (i) of an individual. So

$$G_E = q/i. \qquad \text{(1)}$$

It is necessary for equilibrium of the governing requisite that it should be used at the rate it is generated, in order to prevent its subsequent accumulation or depletion. Commonly a fraction (l) of this requisite is lost to the population, being destroyed by competitive factors; so for equilibrium the amount (lg) of the governing requisite destroyed by these factors, together with the amount ($N_E q$) used by the animals, must equal the amount (g) of the governing requisite generated in unit time. So $lg + N_E q = g$, and therefore the equilibrium density (N_E) of the animals is

$$N_E = (g - lg)/q. \qquad .. \qquad .. \qquad .. \quad (2)$$

It is implicit in equations (1) and (2) that there is no induced mortality, and that depletion of the governing requisite has reduced the reproduction of the animals to the replacement rate. It often happens, however, (as with *L. cuprina*) that animals reproduce at more than the replacement rate even at equilibrium, the surplus offspring produced being destroyed before they can themselves reproduce. These surplus individuals waste a fraction (w) of the governing requisite, in the sense that this fraction is rendered unavailable to those individuals which maintain the population by maturing and reproducing. The effect of this upon the equilibrium density (N_E) of mature animals is clearly

$$N_E = (g - lg - wg)/q. \quad .. \qquad .. \qquad .. \quad (3)$$

As the amount of the requisite so wasted tends to vary directly with the magnitude of the surplus of individuals produced, the greater the reproductive rate the lower tends to be the density of animals permitted to mature.

When predators have prey as the governing requisite they tend to limit this to the threshold density, which is also the equilibrium density of the requisite (G_E), as do animals of any other kind. By so doing they limit the rate of generation (g) of the prey to bG_E at equilibrium, where b is the birth-rate of the prey. This in turn limits the density (N_E) of the predators, for equation (2) becomes

$$N_E = (b - lb)G_E/q. \qquad .. \qquad .. \qquad .. \quad (4)$$

It is clear from equation (4) that the predator density (N_E) is independent of the number of prey individuals required for the maintenance and replacement of the predator individuals, for the value of G_E is proportional to that of q (see equation (1)).

Substituting q/i for G_E (equation (1)), equation (4) becomes

$$N_E = (b - lb)/i, \qquad .. \qquad .. \qquad .. \quad (5)$$

which shows that the greater the efficiency (i) of the predators, the lower is their density. That is to say, the predators reduce the rate of generation of their prey to meet their minimum needs, which are satisfied by a low density (G_E) of prey when their procurement fields (i) are large, and in consequence their own density (N_E) is correspondingly low, being limited to that which can be supported by this low density of prey.

It will be noted that equations (4) and (5) are simply interpretations of equation (2). Even without such interpretation equation (2) represents the necessary conditions for the equilibrium of natural enemies; but as the rate of generation (g) of the governing requisite (the prey) is a function of the birth-rate and of the density of the prey, and as the latter is also a function of the efficiency of the enemies, terms representing these properties are included in expressions which define g, and these are substituted for g in equation (**2**). This permits the components of g to be studied and their separate influences upon population density to be determined in this situation. Examination of other situations lacking the extreme simplicity of those described directly by equations (**1**), (**2**), and (**3**) has indicated that any equilibrium situation can similarly be represented by substituting for one or more of the original terms in these basic equations expressions and new terms which define the original terms.

When the animals considered constitute the governing requisite of natural enemies, equation (**1**) shows that their equilibrium density (G_E) is determined by the properties q and i of these enemies; and when the animals govern themselves by inducing reactions in a governing requisite, equations (**2**) and (**3**) show that their equilibrium density (N_E) is determined by the values of g and l (which primarily represent properties of the environment) and those of q and w (which represent intrinsic properties). Thus g, l, q, w, and i are the *primary parameters of population density,* for it has been found that the influence of any other significant factor upon equilibrium density can be represented in the basic equations (**1**), (**2**), and (**3**) by the change it produces in the value of one or more of these parameters, or by the substitution of interpretative expressions or terms, as in equations (**4**) and (**5**). A more detailed analysis along these lines will be published later.

(*b*) *Population Growth and Maintenance in Simple Situations*

Attention is restricted in this section to populations limited by the reaction of one requisite only, and living in environments which remain constant except in so far as they are influenced by the actions of the animals.

In an environment which remains constantly favourable a population grows unchecked, the population density (N) increasing in time t to $N\mathrm{e}^{(b-d)t}$, the rate of growth at any moment being

$$\mathrm{d}N/\mathrm{d}t = (b-d)N. \quad .. \quad .. \quad .. \quad (\mathbf{6})$$

Here e is the base for natural logarithms, and the coefficients of birth and death (b and d) have values appropriate to the stable age distribution which occurs in any population multiplying without check (Lotka 1925), and so equation (**6**) is true whether the animals are born virtually mature or take an appreciable time to develop to maturity.

However, the environment of a growing population cannot remain constantly favourable indefinitely, for animals progressively deplete some of the things essential for their existence, so ultimately lowering the favourability of the environment to the limit of tolerance. Inevitably it is such environmental reaction to density which limits populations, for animals can exist only when the environment is favourable, and their populations then grow until at least one requisite is reduced to the threshold of favourability, when further growth is impossible. Such reaction of the environment which opposes density change impresses different patterns of population growth and maintenance according to the kind of reaction and the qualities of the reacting requisite, as shown in the accompanying chart (Fig. 6). A primary division is made into *density triggered reaction,* i.e. reaction to density change which remains negligible until the population reaches some critical density, when opposing reaction operates with great violence; and into *density conditioned reaction,* i.e. opposing reaction which progressively increases in intensity with density. The latter is further subdivided in the way shown in Figure 6.

These categories of reaction will be dealt with in turn, subdivisions being made within each according to certain qualities of the reactive requisites. *Persistent requisites* are those which are not expended when used, and invariably consist of some form of favourable space which becomes available again

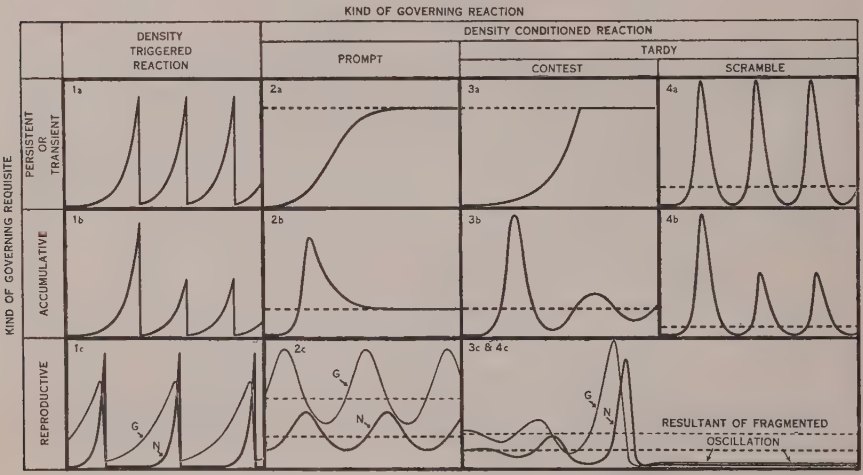


Fig. 6.—These graphs illustrate what are considered to be the characteristic (but not invariable) patterns of population change in the situations indicated. In categories 3 and 4 they represent the densities of mature animals alone. The horizontal broken lines represent the equilibrium densities of the organisms. *N* indicates populations of natural enemies, and *G* those of prey (the governing requisite).

when vacated. *Transient requisites* disappear quickly if not used, and so cannot accumulate; the best example is sunlight — a dominantly important, though transient, requisite for most plants. *Accumulative requisites* when unused remain in the environment for a significant period before disappearing. *Reproductive requisites* do not merely accumulate but multiply when unused. Surprisingly, persistent and transient requisites give rise to the same patterns of population change. This is because a transient requisite (such as a food material which rapidly becomes unavailable if not used promptly) can be regarded simply as a quality of favourable space. It is a quality which determines the population density the space can support, for there is neither accumulation nor multiplication of the requisite to influence this capacity in relation to the recent past history of the animals and their environments.

The classification of basic population systems used in the chart (Fig. 6) is by no means the only possible one, but it is used to illustrate the effects produced by those factors which appear to dominate population regulation. Naturally other factors may influence these patterns, which are described only in their simplest form. Moreover, the systems tend to intergrade, and sometimes population regulation combines the features of more than one of them.

(i) *Density Triggered Reaction.*—It may happen that a population is permitted to grow unchecked until it reaches some critical density at which violent opposing reaction is triggered, so reducing the population to a very low level. The low density of the population then causes reaction to be relaxed, so once more permitting unchecked growth. Such *relaxation oscillation* is thus described by equation (**6**) if a limit is placed to the permissible value of N, and a term is introduced representing the population reduction which takes place whenever this limit is reached. Because of the stable age distribution which occurs in populations when multiplying unchecked, the lag due to the time spent in development by higher animals does not influence the character of relaxation oscillations, except possibly for a short time after the minima.

Relaxation oscillation appears unusual amongst animals and it is doubtful if it ever occurs in the simple form described, for generally conditioned governing reaction plays a part during some phases of growth at least. This is certainly true of the best known examples, namely plague locusts and lemmings. However, these frequently multiply with little check until they reach the critical density at which the majority of individuals migrate in mass away from the favourable regions in which they have developed. Here the requisite is favourable space, and reaction is triggered when it becomes critically crowded and so unfavourable. The consequent relaxation oscillations are represented schematically by 1*a* in Figure 6.

When animals invade a favourable environment in which an expendable requisite has accumulated, they tend strongly to multiply without check until virtually all of this requisite has been removed, when the population necessarily crashes. The requisite then begins to accumulate again, so permitting the population later to multiply from the low level to which it was reduced, so producing a succession of relaxation oscillations which may be expected to be smaller than the initial one produced in the previously uninhabited environment (1*b* in Fig. 6). However, density conditioned governing reaction generally plays some part, at least in the region of the maxima, so causing an approximation to some one of the other *b* systems in the chart.

Relaxation reaction may be produced at times by interaction between two kinds of organisms. For example, certain kinds of moths commonly appear to multiply without check until, when their caterpillars are excessively abundant, there is a devastating outbreak of bacterial disease, which apparently could not make headway previously because of inability to spread in less dense populations. Assuming this explanation, the course of events is shown schematically in 1*c* (Fig. 6), *G* representing the victim species and *N* the disease organism.

(ii) *Prompt Density Conditioned Reaction.*—In its simplest form this is described by the Verhulst-Pearl logistic equation (Pearl 1926), which in its differential form (Gause 1934) is

$$\mathrm{d}N/\mathrm{d}t = N\,(K-N)b/K, \quad \ldots \quad \ldots \quad \ldots \quad (7)$$

where K is the capacity of the environment in units representing places for individual organisms, and b is the coefficient of multiplication of the organisms when free from any effects of crowding.

Extreme promptness of reaction is represented by this equation. Thus, not only are the organisms assumed to multiply at a rate proportional to the still unused fraction $((K-N)/K)$ of the environmental capacity remaining *at that moment,* but the organisms exercise their full influence upon interaction *from the moment they are born*—for the rate of population change is a function of N, differences of properties associated with the ages of individuals being neglected. The main reason for giving further consideration to such remarkable hypothetical organisms is that they have been used to represent animals in some well-known theories of population dynamics which need to be placed in true perspective. However, such considerations may have some bearing upon the dynamics of simple microorganisms which multiply by binary fission, for these have properties approximating to those of the hypothetical organisms; and in addition, they reveal the characteristics of certain fundamental types of interaction when uncomplicated by the effects of developmental lag.

A primary assumption in the logistic equation is that there is a fixed capacity (K) of the environment for organisms of the given kind, such that when these organisms have multiplied to their limit they subsequently remain constantly at their maximum density. It should be particularly noted that this is a postulate in the equation, and not a conclusion. Clearly, therefore, the governing requisite is favourable space, for no other kind of requisite can be used up to a limiting degree and yet retained for use by the organisms. The capacity may, however, be determined by some transient requisite (such as sunlight required by simple algae) which, being continuously generated, gives a constant favourable quality to the space. The situation is that represented by 2*a* in Figure 6.

Another primary assumption is that the rate of multiplication of the organisms at any moment is proportional to $(K-N)/K$, that is to the fraction of favourable space remaining unutilized at that moment. This means that the logistic equation can apply only to special situations in which the rate of population growth is Nb when N is indefinitely small, and is less than this when N increases even slightly. This is an untenable assumption unless application of the logistic equation is expressly restricted to such situations; for it implies that the values of b and K have a particular relation, whereas b and K are determined by independent factors and so may have any relative values according to the circumstances. This simplifying assumption was presumably adopted to avoid discontinuity in the equation; for if K exceeds the density at which the organisms can barely find all they need to multiply at the maximum rate permitted by their intrinsic properties (represented by b) they will multiply exponentially (equation (**6**)) until such time as the favourability of space becomes sufficiently reduced to slow down the rate of multiplication.

It is clear from equation (**7**) that, as b/K is a constant, the assumption has been made that the rate of population change is proportional to the product of N and $K-N$. This shows that N and $K-N$ are not mere numbers, but densities, for it is reasonable to expect the number of contacts promoting multiplication to vary directly with the number of organisms (N) per unit volume and the quantity ($K-N$) of unutilized favourable space per unit volume. On the other hand, with the same number of organisms of a given kind and the same quantity of unutilized favourable space in environments of different sizes, the number of contacts in unit time would inevitably be greater in the smaller environments than in the larger ones.

Because of the postulated relation between the values of b and K already referred to, b/K in the logistic equation represents the fraction of the available space effectively explored by an individual organism in unit time. Consequently, we may put $b/K = i$, i being the *coefficient of interaction,* defined as the procurement field of the organisms measured in the small unit of time used when defining rates of population change. Like b/K, i is a constant, being unaffected by population change.

The logistic equation (**7**) may therefore be rewritten in the notation adopted here as

$$\mathrm{d}N/\mathrm{d}t = iNG, \quad .. \quad .. \quad .. \quad .. \quad (\mathbf{8})$$

for the quantity ($K-N$) of unutilized favourable space per unit volume is the density (G) of the governing requisite.

However, unlike equation (**7**), this equation does not show the dependence of the number of "still vacant places" upon N; but, as any increase in N causes a corresponding decrease in G, this is shown by

$$\mathrm{d}G/\mathrm{d}t = -iNG. \quad .. \quad .. \quad .. \quad (\mathbf{9})$$

As the sum of N and G is always the same (K), the greatest rate of change must take place when $N = G$, i.e. when $N = K/2$. With progressive departure of N and G from equality, the rate of change asymptotically approaches zero, so leading to a symmetrical and sigmoid growth curve (2*a* in Fig. 6).

However, only when the density of animals reaches the level at which there is significant interference between individuals (that is, when iNG is not greater than bN) do equations (**7**), (**8**), and (**9**) begin to apply; but as this generally happens when N is far below $K/2$, the form of the growth curve is but little affected by this factor.

When the governing requisite of the hypothetical organisms is something, such as food, which is expended when used, the population change during any given moment is equivalent to the amount of the requisite obtained less the amount used for maintenance during that moment. That is,

$$\mathrm{d}N/\mathrm{d}t = iNG - qN, \quad .. \quad .. \quad .. \quad \mathbf{(10)}$$

where the density (G) of the requisite is expressed in unit quantities each sufficient to produce an additional organism when obtained by an individual which has already satisfied its maintenance requirements, and the maintenance coefficient (q) is expressed in the same units and represents the maintenance quantum of the requisite in a very small unit of time. Similarly, assuming a constant rate of generation (g) of the governing requisite (also expressed in the same units) the change in density of the requisite during the given moment is equal to the amount produced less the amount used by the organisms. That is,

$$\mathrm{d}G/\mathrm{d}t = g - iNG. \quad .. \quad .. \quad .. \quad \mathbf{(11)}$$

To make a first approximation to real situations it is necessary to introduce a term into equations (**10**) and (**11**) (as with the logistic equation) to represent exponential growth at population densities below the level at which effects of crowding are significant, and also a term to represent the average time of natural persistence of unused particles of the requisite. The graph 2*b* in Figure 6 was calculated using equations embodying these corrections, but its general form can readily be accounted for verbally. Equilibrium is clearly attained when the amount of the requisite used purely for maintenance equals the amount generated, that is, when $qN = g$; but in a previously unoccupied environment there is considerable accumulation of the durable requisite, so initially a growing population greatly overshoots the equilibrium density by using up this accumulation. Subsequently it falls towards it, owing to the depletion of the requisite, either asymptotically or, under certain circumstances, it may execute damped oscillations about this level. Growth approximates the form of the logistic curve only near the limiting situations in which accumulation of the requisite in the absence of organisms is barely above the threshold level for the population (so restricting population density to negligible proportions), or in which the persistence of the requisite is so short that it is virtually transient, so that competition is dominantly for favourable space, as in equations (**8**) and (**9**).

Organisms (such as yeasts) which enter a resting state when the environment approaches the limit of favourability often maintain for long periods the maximum population attained by using up an accumulated durable requisite; but it is illogical to argue from the experimental demonstration of such prolonged existence in a quiescent state (Pearl 1926; Gause 1934) that normal active animals should also maintain constant populations when they reach their maxima.

To examine the interaction of organisms with requisites which reproduce, we will assume that these consist of similar hypothetical organisms; that when a predator (having already satisfied its full maintenance requirements) contacts n prey organisms it undergoes fission, so producing one additional organism; and that the prey has a coefficient of multiplication b. Expressing G and q as numbers of prey (the governing requisite), equations (**10**) and (**11**) then become

$$dN/dt = (iNG - qN)/n, \quad \ldots \quad \ldots \quad \ldots \quad (\mathbf{12})$$

$$dG/dt = bG - iNG. \quad \ldots \quad \ldots \quad \ldots \quad (\mathbf{13})$$

These equations show that for equilibrium $iG = q$, and $b = iN$; so that $G_E = q/i$, and $N_E = b/i$.

Equation (**12**) shows that when G exceeds this equilibrium value the number of prey eaten exceeds the number used in maintenance, and so N must rise; and if it is below this value N must fall. Similarly equation (**13**) shows that if N is above or below its equilibrium value G must respectively fall or rise. Thus when the changing population of either one of the animals passes from above to below its equilibrium value, or vice versa, this reverses the direction of change induced in the other population. Thus a system of *coupled oscillation* is produced (2*c* in Fig. 6), oscillation being due to a linkage between the two changing populations, and not to the operation of lag reactions. In the simple situation examined, the oscillations are found to be sustained at a constant amplitude dependent upon the degree of initial displacement of density.

In form (but not in all the factors involved) equations (**12**) and (**13**) are identical with the basic equations of predator-prey interaction independently developed by Lotka (1925) and Volterra (1931). The assumption of immediate reaction limits even approximate application of the Lotka-Volterra equations to the simplest microorganisms. Their failure to allow for the use of some of the prey for the maintenance of the predators surprisingly does not lead to results differing in character from those derivable from equations (**12**) and (**13**). This is because a coefficient of predator death is used in place of q (equation (**12**)), which also represents an expenditure of material proportional to predator density—but the assumption of a constant inherent death rate is inadmissible when applied to microorganisms which multiply by fission. It is the neglect of the inevitable change in age composition as populations increase and decrease which limits even the approximate application of the Lotka-Volterra equations (and also of equations (**12**) and (**13**)) to exceptionally simple microorganisms, for individuals of these alone amongst animals undergo no important change in properties with age.

Gause (1934), using cultures of *Paramecium* feeding on yeasts, obtained oscillations closely corresponding to the Lotka-Volterra equations. On the other hand, when he used *Didinium* as predator and *Paramecium* as prey, his cultures quickly came to an end, due to the complete destruction of the prey. His figures clearly show that this was due to the unjustifiably small size of the microcosms he used (0.5 ml of liquid medium); for the introduction of only three individuals of *Didinium* into a rapidly growing culture of *Paramecium* was followed immediately by a steep fall in the numbers of the latter, so clearly showing that even three *Didinium* in 0.5 ml of medium must be far above the equilibrium density of this predator. Consequently, cultures of *Didinium* in such minute microcosms would be required to be represented by fractions of an individual as the minima were approached, in order to conform with the equations. That is to say, these experiments did not conform to the conditions necessary for the equations to apply, for these equations represent the statistical effects of the interaction of large numbers of individuals operating in adequate space. Unlike equations (**12**) and (**13**), the Lotka-Volterra equations do not explicitly present space as an essential parameter. The fact that it is implicit to them appears to have been overlooked by Gause when designing his experiments. As to the experiments using much larger microcosms (to which Gause makes passing reference) it would appear that these were initially loaded with such a high density of organisms that vast numbers of *Didinium* individuals, supported by the prey they had already eaten, were still present when *Paramecium* was reduced to a low density, so leading to the complete elimination of *Paramecium*. The result might have been very different had the initial densities of the organisms been low or the available space much greater.

On the basis of these experiments Gause (1934, p. 128) concluded that "in *Paramecium* and *Didinium* the periodic oscillations in the numbers of the predators and of the prey are not a property of the predator-prey interaction itself, as the mathematicians suspected, but apparently occur as a result of constant interferences from without in the development of this interaction." This holds only for the minute microcosms he used. On present evidence it would appear that it was not the mathematics but the experiments which were at fault, for these did not reproduce the conditions postulated in the Lotka-Volterra equations. Gause's experiments with *Paramecium* feeding on yeasts apparently did reproduce these conditions and gave results broadly consistent with the mathematical expectation.

(iii) *Tardy Density Conditioned Reaction* (*Contest*).—Some time always elapses between the event which leads to the birth of an animal and the beginning of significant competition by that animal with other individuals for the necessities of life, this being most marked with the higher animals. It is generally difficult to represent such developmental lag in sufficiently precise terms for mathematical examination, but its effects can be deduced readily by verbal argument, and by the study of experimental and natural populations.

Initially we will confine attention to animals exhibiting developmental lag which *contest* for their requisites; that is to say, an individual either obtains as much of the governing requisite as it needs for survival and reproduction or, being unsuccessful, relinquishes the requisite to its successful competitors. Thus with contest all of the governing requisite collectively secured by animals is used effectively in maintaining the population.

If the requisite consists of a fixed quantity of available space, the situation is most easily represented by plants competing for sunlit space. When a plant species invades a new and favourable area, population growth is at first exponential, the population consisting dominantly of young individuals. By the time crowding significantly impedes further population increase, the number of individuals greatly exceeds the number of mature plants the space can accommodate, for the space requirements of young plants are small. Subsequently there is a fall in density as the more powerful, or more fortunate, maturing individuals displace their neighbours, until equilibrium is reached when the only space available to young individuals is that vacated by the dead. Thus the growth pattern of the total population should resemble graph 2*b* (Fig. 6), whereas that of mature individuals is represented schematically by graph 3*a*, for their density progressively increases with little check until they completely fill the available space. Populations of animals with sessile or territorial habits may have similar growth patterns.

If the requisite consists of expendable but durable objects these, being generated at a constant rate, inevitably accumulate in an unoccupied region, so leading to an exceptionally high density of animals shortly after introduction. Subsequently reactive changes in the density of the requisite always tend to cause the population to approach its equilibrium density; but, as the effects of this reaction always lag for the time taken in development, density change is not arrested when this level is reached, but continues beyond it, thus leading to *lag oscillation* (3*b* in Fig. 6). This situation is of doubtful importance, for animals seldom contest for non-persistent objects other than prey.

Volterra (1931) discussed the effects of substituting lag reactions ("actions héréditaires") for the immediate reactions assumed in the basic part of his study of the interaction of predators and prey, but the biological meaning of his conclusions is obscure. He retains the assumption that increase in predators and decrease in prey are directly proportional to the number of contacts between them. Thus his primary assumptions were essentially the same as those of Nicholson (1933) and Nicholson and Bailey (1935) (although his mathematical models were quite different), for the only kinds of predators and prey which approximate to his premises are lethal "parasites" of the insect type and their "hosts." When such a "parasite" lays an egg it provides its offspring with all it needs for full development, and usually some mechanism reserves the attacked "host" for the exclusive use of the parasite larva. Competition is therefore of the contest type. For this reason, and the additional fact that entomophagous parasites commonly develop large numbers of eggs, we can assume (as a first approximation) that the number of hosts destroyed and the number of parasite offspring produced are proportional to the number of contacts between parasites and unparasitized hosts, so making mathematical analysis simpler than with other types of predators and prey. In this system oscillations are produced which are due to both coupling and lag effects. In simple situations such *coupled-lag oscillations* (3*c*, Fig. 6) were shown by Nicholson and Bailey to increase in amplitude with time.

Such systems of growing oscillation are inevitably self-destructive, for limitless growth in amplitude is clearly impossible. The depletion of some requisite by the hosts when they reach high densities may prevent the peaks of the host oscillations from rising above a certain density, so converting the system into one of sustained oscillation. If this does not happen the distribution of the population inevitably becomes discontinuous when the minima become very low, for individual families of animals must often be widely separated. If the descendants of each family do not disperse readily they form an isolated group which interacts independently with any parasites associated with it, and so a system of *fragmented oscillations* is created (Nicholson 1933, 1947; Nicholson and Bailey 1935). At any moment some groups of individuals are growing unchecked while others are in process of extinction by parasites, and migration of both hosts and parasites into unoccupied areas takes place all the time, so giving rise to new centres of oscillation. Such fragmented and changing distribution of hosts at a very low average density appears to be characteristic of control by really effective parasites (Nicholson 1947).

Varley (1947, p. 181) has claimed that "it can be shown with Nicholson and Bailey's theory that if a proportion of hosts is not available to parasitism, oscillations will be damped instead of increasing with amplitude." This is an overstatement, for the examination of numerical models has shown that oscillations grow in amplitude with time even when a considerable fraction of the surviving animals live in protected situations. In fact, it was found necessary to assume quite low powers of increase of the hosts, and the protection of the greater part of the fraction of hosts required to survive for population maintenance, before the postulated damping could be obtained—and if more than this fraction is so protected the parasites naturally cease to be capable of governing host density.

If some host individuals are more difficult to find than others, i.e. if the area of discovery (the procurement field) of the parasites is greater for some hosts than for others, the proportion of "difficult" to "easy" hosts in the population naturally increases with increased destruction. Although this tends to lessen the rate of growth of successive oscillations, numerical examples have indicated that only when the area of discovery for the "easy" hosts is many times as great as that for the "difficult," and when the power of increase is low, is it possible to convert the system into one of damped oscillation. Thus the tendency for populations of interacting parasites and hosts to exhibit growing oscillations is very great, and the erratic and ever-changing fragmented distribution of many insects, notably sessile ones, strongly suggests that population systems which are basically of the growing oscillation type (3*c*, Fig. 6) are common in nature (Nicholson 1947).

(iv) *Tardy Density Conditioned Reaction* (*Scramble*).—The characteristic of "scramble" is that success is commonly incomplete, so that some, and at times all, of the requisite secured by the competing animals takes no part in sustaining the population, being dissipated by individuals which obtain insufficient for survival.

Examples of populations governed by the depletion of a requisite for which they scramble are the cultures of *L. cuprina* already referred to (see Figs. 3, 4, and 5), and details of the governing mechanism have been given. Reaction is of the right kind to compensate for overcrowding, but, owing to the time taken for the offspring to develop, the effects of the high mortality or low natality caused at high densities continue for some time after the population has reached its equilibrium density. Thus lag oscillations are produced and these are more violent than in situation 3*b* (Fig. 6), for high densities do not merely cause great depletion of the requisite but also great wastage. If the intrinsic birth-rate is very low an asymptotic approach to the limiting density is probable (Nicholson 1948).

Schematic representations of such lag oscillations are shown in Figure 6 for animals governed by transient requisites (4*a*) and by accumulative requisites (4*b*), the only important difference being an accentuation of the violence of oscillation due to effects of intermittent requisite accumulation in system 4*b*, particularly initially.

The mathematical models created for predators of the protozoan (Lotka 1925; Volterra 1931) and entomophagous parasite (Nicholson and Bailey 1935) types and their prey do not apply directly to predators which scramble for their prey (such as birds of prey and carnivores), for the assumed direct relation between the number of contacts and the number of predator offspring produced is not even a reasonable approximation to reality. However, from the character of the interaction with prey one would expect oscillation of the coupled-lag type (3*c*, Fig. 6); and that this sometimes occurs is strongly suggested by the fact that fragmented distribution of *Icerya purchasi* in California, and of *Opuntia inermis* in Australia, was observed to result from the introduction respectively of *Rhodolia cardinalis* and of *Cactoblastis cactorum* (Nicholson 1947). The fact that such fragmented oscillation is unusual in populations of the higher animals strongly suggests that vertebrate predators are seldom the primary governing factors of their prey. Often they appear to be little more than the destructive instruments of some governing requisite—as when the depletion of food or of favourable space weakens the prey or drives them from their refuges, so permitting them to be attacked by predators, which they would otherwise escape (Nicholson 1947).

V. Population Regulation in Complex Situations

(*a*) *Climatic Influences*

For ease of analysis attention has so far been restricted to populations living under constant conditions—constant except insofar as they are affected by the actions of the animals themselves, or by the influence of a newly introduced factor under consideration. Such constancy of conditions is seldom approached in nature. For example, there is commonly a wide variation of climatic conditions with the seasons, and of climatic conditions in different parts of the range of any given species.

It has often been claimed that climate is dominantly responsible for the regulation of populations. This is probably true if "regulation" is used in the rule-making sense alone, for climatic conditions not only have a great direct influence upon the well-being of animals, but they are ultimately largely responsible for determining the composition of the communities in which they live.

In other words, climate may greatly influence the values of the primary density parameters, and by so doing affect the level at which governing factors adjust the densities of populations. On the other hand, climatic conditions are unaffected by any changes in the densities of the animals subject to them; and so, being unable to react to density change, they cannot govern populations, although they may have a profound legislative influence upon population densities.

It sometimes happens, however, that the densities of animals are governed by reactions of microclimates. For example, some insect pests of stored grain limit their densities by raising the prevailing temperature or humidity to barely tolerable levels.

To show why climate cannot govern population densities, let us assume that all other factors in the environment are also non-reactive. If, then, all conditions are favourable to animals of a given kind, their population will grow without check, and so, in any long period of time, the animals will increase to indefinitely large numbers. This is true even though the permitted rate of geometrical increase is very low, and irrespective of whether the environment remains constant or fluctuates violently about this average favourable level. Conversely, if the conditions are unfavourable, however slightly, the population must tend towards extinction in any long period of time. Even if the degree of favourability were maintained at the minimum, so just permitting the bare replacement of animals as they die, the absolute density would be independent of the environment, being simply the initial density in a constant environment, or fluctuating about this density in a fluctuating environment. In fact, in all three situations the absolute density at any moment would be merely a function of the initial density and of the subsequent history of increase and decrease in relation to the varying favourability of the environment. Change in density would be related to change in favourability; but absolute density would be independent of the conditions prevailing at any moment.

The fact that population levels are observed to be related to the climatic favourability of environments has often been claimed to show that the climate itself determines population levels. This view is untenable, for it is evident from the considerations just presented that the existence of this relation proves that there must be some governing mechanism in the environments which climate can influence in order to produce it; for climate itself merely permits population increase or causes decrease, according to its favourability or otherwise.

Although true equilibrium is impossible under fluctuating conditions, there is at each moment a density level which, if it were attained by the population, and if the environmental conditions prevailing at that moment were to persist, would cause the environmental forces opposing density change, including those induced by the population, to exactly counterbalance the properties of the population favouring multiplication. Consequently, it can be said that the level of equilibrium density fluctuates in association with environmental fluctuations, through the effects these have upon the properties of animals and those of their requisites. Reactions tending to cause increase or decrease are produced respectively when a population is below or above the equilibrium density appropriate to the conditions prevailing at each moment. Consequently, reaction holds populations in leash to the ever-changing levels of their equilibrium densities. Although such influences as developmental lag, and the coupling of prey populations with those of their predators, may cause oscillations of internal origin, reaction forces such oscillations to take place about the equilibrium levels which change with the changing environment.

The situation is complicated by the fact that any marked climatic changes produce very noticeable direct effects upon population densities. In addition, any periodic change of climate tends to impose its period upon oscillations of internal origin, or to cause such oscillations to have a harmonic relation to periodic climatic changes. For example, if the natural period of oscillation under constant conditions were more than 1½ and less than 2½ years, there is reason to believe that seasonal influences would cause peaks of abundance to occur regularly every 2 years. This is because the phase of growth is likely to be prolonged when conditions are very unfavourable, whereas if this phase coincides with very favourable conditions it would be passed through quickly; so there is a strong tendency for the increasing and decreasing phases of oscillation to coincide in time with external conditions which favour them, provided these external influences are powerful.

General considerations and the examination of numerical examples have indicated that, although the period of climatic oscillation may be imposed upon oscillations of internal origin, the violence of population change is likely to be much greater than that which would be produced by, say, seasonal change alone. That is to say, the actual variation in population density tends to be much greater than the variation in its equilibrium level (Nicholson 1933, C.73, C.74, C.75, and Fig. 11). Thus reaction between populations and their governing requisites is probably largely responsible for the violence of population fluctuations in nature; but, because these fluctuations strongly tend to coincide in time with environmental changes in favourability, there is a natural tendency to conclude that population densities are wholly determined by the varying physical environment. The very existence of oscillation of internal origin is masked by synchronization with periodic external changes.

If the fluctuating conditions are definitely unfavourable at times, a population progressively decreases during those times, but at the intermittent favourable periods the population tends to adjust itself to the prevailing conditions. This determines the density at the beginning of each unfavourable period and therefore also the general level from which the population falls during these periods. Density governance is merely relaxed from time to time and subsequently resumed, and it remains the influence which adjusts population densities in relation to environmental favourability.

In spite of their inability to govern population densities, climatic factors have an influence of outstanding importance upon populations, but their influence is purely legislative. This influence can be represented in the basic equations by appropriate changes in the values of one or more of the primary parameters.

With field populations the analysis of such influences is greatly complicated by the fact that an environmental change may do more than alter the values of the primary parameters, for it may also cause the attribute of being in shortest supply to be transferred from one depletable requisite to another. Consequently, the same species population may be governed by the depletion or impairment of different requisites at different times in the same place, or in different parts of its distribution area at the same time. These complexities do not affect the validity of the equilibrium equations, for no matter what may be the identity of the governing requisite, the appropriate values of g, q, w, l, and i together represent the collective influence of the environmental and intrinsic factors on equilibrium densities—but with fluctuating conditions, the identity of the governing requisite represented by these parameters may change from time to time.

(*b*) *Edaphic Influences*

Although the nature of the soil and the characteristics of the land surface seldom directly affect animal populations, they do so indirectly by profoundly influencing the composition of the plant communities in different places. This frequently leads to a mosaic of widely varying environments within which the habitat of a given species exists only in widely separated patches. Most species are well adapted to cope with such fragmentation of their habitats. They have a more or less defined dispersal stage, during which they readily move out of their true habitats, sometimes to great distances, and they also have the ability to recognize favourable situations when they are encountered. These adaptations are particularly significant when conditions which contribute to an animal's habitat are ephemeral, and when different life-stages occupy different habitats, for species lacking these properties would often be unable to find some of the favourable parts of the region in which they occur.

The unfavourable environments which animals encounter when they stray from their proper habitat commonly do not menace the animals, for generally they merely lack some particular requisite, such as food or oviposition sites. Consequently the adaptations just mentioned enable animals to occupy fully all favourable sites, and the fragmentation of their habitats has little effect upon their well-being. The populations are governed by density reactions within these favourable sites, these being the only places in which competition is significant. This is true whether the unsuccessful animals remain within the true habitats or disperse into the surrounding unfavourable country. In the second situation the cause of death or of inability to produce offspring may appear to be the unfavourability of the conditions to which the animals are subject, but this is only a secondary effect of the competition within favourable sites which forced out the unsuccessful animals.

Thompson (1939, p. 338) claimed that "the discontinuity and variability in habitats, produced by the physical factors both in time and in space, is undoubtedly the primary extrinsic factor of natural control". In support of this conclusion he asserted that when an organism "increases in numbers it necessarily spreads, both in space and time. As it spreads it moves to points outside its optimum environment, when its rate of multiplication immediately diminishes". However, more critical examination shows that multiplication throughout the occupied area cannot be reduced in this way to the bare replacement rate, as is necessary for population limitation.

As Thompson's arguments imply that the spread of organisms is unaffected either by the degree of favourability of the environment or by population density, it is clear that he postulates random movement of the constituent organisms. In these circumstances, populations could not spread appreciably beyond the border zone of minimum favourability, the characteristic of which is that the fraction of organisms born there which is lost by random movement into the neighbouring unfavourable areas equals the fraction of organisms which is surplus. In all less favourable areas the organisms would multiply less rapidly and so could not maintain their numbers (the rate of diffusion by hypothesis being a constant). On the other hand, in all more favourable zones the rate of multiplication would be greater, and so the fraction of offspring lost by diffusion from them would be less than the surplus produced. The resultant growth of the population in such areas would be augmented by diffusion into them of some of the offspring born in neighbouring favourable areas. That is to say, the population would grow without check in all favourable areas other than those on the border line of favourability. Inevitably overcrowding would soon occur throughout most of the occupied area, so leading to limitation by competition.

Similar arguments apply to the spread of populations in time, and they are well illustrated by the numerical example Thompson (1939, p. 339) used in an attempt to show that the spread of a population causes a progressive fall in the rate of multiplication. Thompson terminated the examination of this example at the second generation, but when it is continued into subsequent generations it at once becomes clear that the population within the favourable period continues to multiply at a rate exceeding that of geometrical increase, and that the fate of the animals occurring during the unfavourable period has no influence upon this rate of increase.

The reason for the great difference between the diffusion patterns of inanimate objects, such as gas molecules, and those of organisms is that the latter have finite lives. The new organisms which continue the diffusion after others die necessarily begin their operations within the favourable areas in which they were born. This inevitably restricts the ultimate distribution of the population to the favourable areas plus a surrounding unfavourable zone, no part of which is at a greater distance from some favourable area than that which can be traversed by an individual during its lifetime. Consequently, spread into unfavourable areas is definitely restricted by the distribution of favourable conditions, and it cannot continue to increase progressively so long as more than the replacement number of offspring is produced by the organisms, as Thompson postulated.

(*c*) *Biotic Influences*

Animals which are directly dependent upon plants may govern the densities of their food plants, and so also their own densities; but more often they are governed by other factors at densities which cause them to have little, if any, influence upon the densities of their food plants. Plants influence animals not only by providing them directly or indirectly with food, but also by determining in large measure the composition of the communities in which they live, by satisfying special requirements, such as nesting sites and refuges, and by providing favourable microclimates.

Animals are influenced by other animals in many different ways. The densities of some are directly influenced by those of the animals they are dependent upon, whereas they have little or no influence upon the densities of their benefactors. Examples are epizoic, coprophagous, and commensal animals, and benign parasites. A few are symbiotic and so tend to increase the densities of their partners. More often animals adversely affect animals of other species. Pathogenic organisms and predators (including "parasites" of the entomophagous kind) destroy their hosts or prey, and by so doing may limit their own populations as well as those of the animals upon which they are dependent. As has already been shown, there is a strong tendency for such interaction to lead to periodic oscillations in density. When the predators attack several species of prey and the prey species are attacked by several species of predator, the periodic oscillations in density each pair of interacting species tends to produce inevitably interfere, sometimes opposing and sometimes assisting one another. In this way erratic and aperiodic oscillation in density is likely to be produced, and to be made still more complex by the influence of varying climatic conditions.

Under natural conditions populations are not only subjected to the disturbing influence of fluctuating climatic factors and of various destructive agencies, but they have to exist together with populations of other animals which require some at least of the same requisites. Now, for the contemporaneous existence of several different species in the same place, each species must possess some advantage over all the others with respect to some one, or group, of depletable requisites, and in addition be able to tolerate the depletion of other requisites which is caused by competing species (Nicholson 1933, C.2). The reason for this is that each species must govern the density of at least one such requisite in order to govern itself, so excluding the possibility of any other species governing (and so being governed by) the reaction of the same requisite. It will be observed that this conclusion defines the necessary conditions which determine whether two or more species can live together or not, in contrast to "Gause's hypothesis" which, according to Lack (1947) is that "two species with similar ecology cannot live together" (see Gilbert, Reynoldson, and Hobart 1952).

Implicit to this conclusion are the important qualifications that all the species are restricted to the area within which they compete, and that environmental conditions are constant throughout this area. This is often not true, for environmental conditions change from place to place, often within very small areas, and it may well happen that each of the competing species has an advantage over all the others in certain parts of the region in which they occur. If there were no diffusion of the populations, each species would exclude the others from those parts of the region in which it is most potent. Normally, however, there is such diffusion, and consequently intermingling of populations of different species with similar requirements should be a permanent situation, in parts of the environment at least. This is because the tendency for each species to displace the others from the places in which it is most potent is continually countered by immigration of new individuals of the other species from those parts of the environment in which they in their turn are most potent.

It is evident that fluctuations and oscillations in abundance of different species living together should often interfere with one another, this being most marked when two or more species influence the abundance or availability of a common requisite, or the density of a polyphagous natural enemy. The oscillations of internal origin should sometimes oppose and sometimes augment one another, so causing irregularity in the time of occurrence and in the magnitude of the peaks of abundance of any one species. Seasonal changes should still tend to impose their period upon the populations, but the effects of interference would be to cause many apparently erratic changes in the populations unrelated to any external change.

It should be noted that, although some factors act merely as the instruments of destruction employed by some governing factor, they are generally legislative factors and may produce important effects upon density levels. For example, many vertebrate predators seem capable of attacking only those prey individuals which are weakened by dearth of food or by age, or which have been forced by population pressure to leave the refuge of their natural habitats. At first sight it might appear that in this situation the predators merely destroy individuals which are already doomed to death from other causes, and that consequently they should produce no significant effect upon the density of their prey. This is far from true, for it is notable that such destruction tends to limit the prey population at near the highest level their pasture can support. Were it not for the destruction of semi-starved prey by the predators, populations of herbivorous animals would reduce their food to extreme scarcity, so leading to a fragmented distribution of both herbivores and their food plants at very low average densities (Fig. 6, situation 4*c*).

This raises a very important question. Almost all kinds of plants are attacked by one or more species of animals, and animals tend to reduce their food supplies to the threshold density at which they can barely find enough food to maintain themselves and to produce sufficient offspring to replace them at death. With most kinds of herbivorous animals this would lead to an extremely sparse distribution of their food plants—yet observation indicates that terrestrial plants succeed in occupying fully practically every site in which conditions are suitable for plant growth. The question is, how can these apparently contradictory conclusions be reconciled?

Sometimes herbivorous animals do limit their densities by reducing their host plants to such scarcity that they have great difficulty in finding them, as happened as a result of the introduction of *Cactoblastis cactorum* into Australia to attack *Opuntia* spp. (Dodd 1936) and of the introduction of *Liothrips urichi* into Fiji to attack *Clidemia hirta* (Simmonds 1937). It is possible that such fragmented distribution of plants caused by the action of their enemies (notably insects) is far commoner than is realized, for the influence of the enemies is inconspicuous when balance exists and both insects and their host plants are scarce and widely scattered. However, it is quite evident that this situation is not general, and that usually animals are prevented by other factors from directly limiting their food supplies. One mechanism is the destruction of weakened herbivores by natural enemies, in the way already referred to, which prevents the eating out of pastures and causes the herbivores to maintain populations near the maximum density the pastures could possibly support. Insect enemies of plants, on the other hand, appear generally to be reduced by their own enemies to the threshold level for these, which commonly means that their effect upon plants is not very significant. Probably many factors other than the availability of their food plants and the attack of natural enemies limit the populations of some plant-eating animals, but there seems very little doubt that the major influence which prevents animals reducing vegetation on the earth to extreme sparseness is the attack of phytophagous animals by enemies of their own.

(*d*) *Population Balance*

In spite of the violence and complexity of population changes produced by the interaction of different systems of population oscillation of internal origin and the influence of climatic changes upon these, it is clear that the underlying mechanism is one of balance. The densities (N) of populations and those (G) of their governing requisites are counterposed, and any change in these quantities (whether produced by the environment or by the action of the population itself) sets up reactions which tend to cause approach to a condition of equilibrium.

The balance a population maintains in spite of the varying conditions in its environment can be likened to that of an equestrienne dancing on the back of a horse cantering round a circus ring: her movement is partly due to her own action and partly to that of the horse, and she remains poised upon the horse's back by expertly adjusted compensatory reactions to all the disturbances which tend to cause her to fall. The persistence of populations in their ever-changing environments, and their maintenance of degrees of abundance in general conformity with the changing conditions, are wholly dependent upon compensatory reaction to external forces.

The conclusion that populations govern themselves by inducing the environmental resistance which limits their densities in relation to prevailing conditions is the antithesis of Chapman's (1931) theory of "biotic potential," which postulates that resistance is purely a characteristic of the environment, and that the properties of organisms are adjusted to this, presumably by the process of evolution. Even if such precise adjustment of properties were produced, it could not adjust population densities in relation to environmental conditions, for the properties of the animals would then be in a state of equilibrium with those of their environment at any density (Nicholson 1927, 1933).

If populations were dependent upon such qualitative adjustment of their properties to those of their environments, pest control would be far easier than it has proved to be. It would merely be necessary to apply a control measure to reduce the pest population to, say, 1 per cent., and then, without any further action, population density at any subsequent time would be only 1 per cent. of what it would otherwise have been! In fact, pest control by chemical means has demonstrated conclusively and on a vast scale that the rate of growth of populations is influenced by their densities. When no measures are taken to control pests which are well established, their populations are never in a continuous state of progressive growth. After the first application of insecticides, however, the pest populations invariably begin to grow very rapidly from the low levels to which they have been reduced, and they soon reach densities which make it imperative to apply insecticides once more. This process must be repeated at intervals in order to maintain control of the pests. Evidently the factors which previously checked population growth have automatically relaxed their influence.

(*e*) *Economic Control of Pests*

When considering the imposition of new destructive factors upon populations living in simple situations, it was shown that the populations automatically accommodate themselves to the new situations, provided the destructive factors continue to operate. When a state of balance is re-established after the introduction of a destructive factor the total mortality is adjusted to 100 per cent., just as it was when the destructive factor did not operate, for density reactive factors relax their action to make place for the destruction caused by the new factor. In doing this they cause more individuals to reach the life stage of the animals affected by the new factor (Table 1). Consequently, when balance is re-established, the number of animals in the stage surviving destruction is greater than it was when the new factor first operated (although less than before the destructive factor operated), and the density of animals at some other stages may even be increased, as has been shown.

That new destructive factors do not add to mortality in the long run, but merely change the distribution of mortality, and that reaction always tends to counteract the immediate effects upon density produced by such factors, are facts which must be taken into account seriously when considering problems of pest control. They probably in part account for the common experience that control measures often do not maintain the effectiveness obtained when they were first tried. It is important to recognize, however, that in the examples upon which these conclusions were based the governing function was exercised by the same factor before and after the introduction of the destructive factor. There is good reason to believe that when control measures are effective this is because they have taken over the governing function, and have reduced the original governing factors to purely legislative status. Such displacement of the original governing system has its dangers, for any relaxation of the control measures is likely to lead to a serious outbreak of the pest which is likely to reach a density far above that which existed before control was applied. Developmental lag permits this to occur before the original governing factors react sufficiently to check population growth and subsequently to re-establish the original state of balance.

Similarly it seems improbable that introduced natural enemies can exercise effective control of a pest unless they take over the governing function; and, as has already been mentioned, they are most likely to be effective if their interaction establishes a system of growing oscillations which leads to fragmented distribution of both natural enemy and prey. The establishment of such systems is frequently prevented by an imperfect correspondence in time or in space between the occurrence of enemies and their prey. For example, the seasonal period during which insect parasites of a given species hunt for their hosts may not completely coincide with the period during which their hosts are in a suitable stage to attack, so that hosts which reach the vulnerable stage during certain periods are completely free from attack. This leads to outbreaks of hosts at certain times of the year, which are terminated after the parasites come into action. The immunity to attack of part of the host population reduces the average efficiency of the parasites in finding hosts. As this is equivalent to reducing the value of the procurement field (i), this leads to an increase in the densities of both parasites and hosts (see equations (**4**) and (**5**)). Such imperfect correspondence between the time or place of operation of a parasite and the time or place at which the vulnerable stage of the host exists is probably one of the most important causes of inefficient control by parasites. It may well lead to such high densities of the hosts that these cease to be governed by the parasite—the governing function being taken over by some other factor (such as the food supply of the host), and the parasite density becoming a purely legislative factor.

(*f*) *Natural Selection*

It is generally agreed that natural selection has played a very important part in the development of the highly organized communities which make such complete use of the inhabitable parts of the land surface, and it should be noted that balance due to density governance is an important part of the mechanism of natural selection. It tends to hold the intensity of reaction at the level which just counteracts the innate ability of a population to grow. This induced intensity, being adjusted to the average properties of the individuals, is insufficient to prevent the growth in numbers of individuals with advantageous properties, whereas it is too powerful to permit the other individuals to maintain their numbers. As individuals of the favoured kind increase in numbers, the intensity of reaction progressively increases towards the value which counterbalances their properties, so slowing down their own rate of multiplication and accelerating the displacement of individuals to the original less potent kind, which are therefore forced to extinction (Nicholson 1927, 1933).

A point of considerable interest revealed by the present study of the mechanics of population regulation is that natural selection does not necessarily favour the success of the species, in the sense of increasing its abundance. For example, if within the population of an entomophagous parasite there were some individuals which were more efficient than the remainder in finding hosts, they would unquestionably find more hosts and so have more offspring. Consequently their descendants would progressively displace those of the less efficient individuals. But increased efficiency means that the procurement field (i)

is relatively large, and it will be seen from equation (**5**) that the selection of this advantageous property reduces the equilibrium density of the parasites possessing it. Similarly, equations (**1**) and (**4**) taken together show that if because some individuals required fewer prey for maintenance and replacement (q is reduced) they and their descendants displaced the others, the equilibrium density of the predators would remain unchanged by the selection of this advantageous property: and equation (**3**) shows that the selection of the offspring of individuals with a greater than average reproductive capacity (which would be inevitable if other properties remained unaltered) would reduce the equilibrium density of mature animals, for the increased surplus of offspring produced would cause a greater wastage of food by those individuals which are prevented from maturing (w increased).

These considerations confirm the conclusions reached elsewhere (Nicholson 1927) that natural selection preserves individuals with advantageous properties without reference to the success of the species, and that the elimination of individuals which do not possess these advantageous properties is due to automatic intensification of environmental reaction resulting from the changed properties of the population which selection has caused.

It should be noted that the selection of advantageous properties in one species may cause it to deplete some requisite it shares with another to below the threshold density for the competing species, which it therefore displaces. So, natural selection continually tends to disturb population balance by improving the properties of competing species, instead of producing balance, as it is often supposed to do.

On the other hand, the improved properties selected may enable a species to extend its geographical or ecological range, or to break up into daughter species if the selective influences are different in different parts of its range. Thus the properties of animals, and also the compositions of the communities to which they belong, are largely resultants of the selective influence of density governance when operating over long periods; and this in turn has an important influence upon features of the physical environment, such as microclimates.

(*g*) *Population Dynamics*

In brief, by providing a mechanism which causes well-adapted organisms to be completely displaced by those with even slightly better adaptation, the self-governing reactions of populations in large measure determine the properties of organisms and those of the communities to which they belong; and in addition, they adjust the densities of populations in relation to these properties and those of the physical environment. As the considerations given in the earlier parts of this article show that the underlying mechanism of self-governing reaction almost always is competition, there can be little doubt that competition is the major force which regulates the amount of matter and associated energy taken up from the environment by communities of organisms, and which also determines the course which this takes through populations of different species before being returned to the inorganic environment.

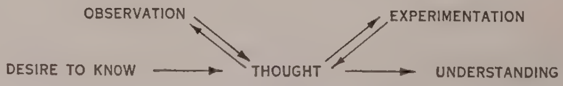
VI. Critical Review of Evidence and its Interpretation

(*a*) *The Place of Thought in Research*

The foregoing discourse begins with the statement of certain facts of common knowledge which are so well established as to be incontrovertible. The implications of these facts are examined in relation first to very simple situations, and then to progressively more complex ones, and eventually general conclusions are reached concerning population growth and maintenance under natural conditions. Although much use is made throughout of further evidence derived from observations and experiments, the method of investigation is essentially deductive reasoning. The approach is thus the same as that used in earlier articles (Nicholson 1933; Nicholson and Bailey 1935); so, as this has been seriously criticized by certain biologists, notably Thompson (1939) and Ullyett (1953), it is necessary to examine its validity.

In particular Thompson and Ullyett criticize the deductive use of mathematics in investigations of population problems—an approach which they consider unsound. Epitomizing his views Thompson (1948) said, "It is a mistake to imagine that by any mathematical subterfuges, we can dispense with direct contact with nature. Observation and experiment must remain the basic elements of entomological science." Taking it at its face value, no biologist would deny the evident truth of this assertion; but it contains the unjustifiable implication that when mathematics have been used for the study of population problems the postulates used have not been based upon ascertained fact. This is not true of most mathematical investigations—although there are a few notable exceptions. The omission of thought as one of "the basic elements of entomological science" is probably not due to this element being taken for granted (as might be argued), but rather to the fact that its supreme importance is all too frequently ignored by biologists working in this field. The common and reiterated insistence upon the paramount importance of observation and experiment, and the deprecation of "theorizing" (which seems to be the fashionable word for any deliberate and sustained thought) indicates a gross misunderstanding of scientific method. There appears to be a widespread idea that the facts of nature can be revealed by observation and experiment alone, so avoiding both the pitfalls and labour of thought; and the history of the investigation of the problems presented by populations certainly supports this surmise. Misconceptions upon this subject appear sufficiently widespread to justify a brief discussion of the relation between observation, experimentation, and thought.

The course of any sound investigation can be represented diagrammatically as follows:



Investigation necessarily begins in the mind and (in the natural sciences at least) the first step is to find what actually happens in nature. Initially this generally consists of reviewing pertinent data already collected, and then making new observations to check, and to add to, the facts already known. Not only is thought necessary in the selection of the field to be studied, but also in the selection of the kind of observations to be made; for, no matter how complete one may attempt to make the observations, only a chosen few of the things that occur and happen are in fact recorded. In this way additional information is gathered which on consideration suggests lines for further investigation. Whether this takes the form of a more intensive study of the facts already gathered, or of further observation, or of experiment, depends upon one's assessment of the situation. In general, one should first extract all possible information from the available data to obtain the maximum guidance for further observation and experimentation; and one should make observations in the field, in preference to laboratory experiments, when these can provide the information sought—for facts so revealed can be seen in their proper context. The observational method, however, has serious limitations, for the things observed and recorded are commonly the resultants of the interaction of many factors whose separate influences cannot readily be disentangled. Many different interpretations of the observations may be possible. The observer may fail to recognize some of the possibilities, and there is a strong tendency for him to attribute the cause of the things he observes to some particular influence which he happens to be studying, or which he subconsciously prefers. Statistical analysis may help to disentangle the roles of the various influences; but often the only way to do so is to maintain most of the variables constant in laboratory experiments, so enabling one to study the effects produced by the various influences acting singly, or in small manageable groups. The precise results so obtained can be used to elucidate field observations, or to formulate new hypotheses worth testing. The experimental method has the further advantage that it is concerned with the characteristics of mechanisms and with the effects they produce under given conditions, and so the conclusions reached can be applied to populations of animals of any kind which are influenced by the same mechanisms.

Thus a necessary condition for investigation is a continual interplay between thought and observation or experimentation, which leads eventually to understanding. In any sound investigation thought must occupy a central and dominating position. It must be honest and accurate, and disciplined in the highest degree. It must precede and follow each active step in observation and experiment; and when an understanding of the immediate problem has been achieved, the discipline of thought must be studiously maintained, for much confusion has been caused in biology by extrapolating sound conclusions to fields in which the basic considerations upon which they were based do not apply.

As mathematics is an exceptionally powerful tool of thought, this method should be used wherever it is applicable. It is true that it does no more than reveal clearly relations which are implicit in the postulates used, but it commonly does this with greater precision than any other form of thought, and it often reveals things which would remain hidden without its aid. The truth of the conclusions reached is necessarily dependent upon that of the postulates. Consequently if field observations give results at variance with mathematically derived conclusions, the error does not lie with the mathematics, but must be due to the postulates being inapplicable to the situations studied. It is therefore critically important to base the postulates upon facts so firmly established by observation and experiment as to be unquestionably true. However, much progress can often be made by using terms in the equations which are only first approximations, as, for example, by assuming a particular relation between population density and the intensity of environmental reaction which is known to be at least approximately true for some animals. The results so obtained form useful guiding hypotheses for further investigation. The mathematical method is not an alternative to observation and experiment but is necessarily a supplement.

(*b*) *Critical Review of Some Population Theories*

Although I agree heartily with the view that there is an urgent need for more intensive observation and experiment in order to acquire knowledge of populations and of the mechanisms which control them, and although no one could be more critical of the use of "theorizing" (in the sense of loose and ill-founded conjecture) as a means of reaching understanding, a study of the investigations of population problems which have so far been carried out has forced me to the conclusion that the greatest present need is for greater clarity of thought, not only in the formulation of hypotheses and theories, but also in the collection and interpretation of data.

In general biologists are prepared to expend almost unlimited time and labour in the collection of data; but only too often they give surprisingly little thought to the questions of what kinds of data need to be collected to throw light upon the problem under investigation, and of the true implications of the data when they are collected. For example, certain investigators have expended great effort in determining the percentage destruction caused by each of a number of factors which influence populations of a given animal and (confusing their hasty conclusion with ascertained fact) have claimed that the particular factor which causes greatest destruction is dominantly responsible for the limitation of population density. A little thought along the lines given in earlier parts of this article would have shown that no direct relation between percentage destruction and population density can be expected, and that therefore, not only is the conclusion unjustified, but so also is the collection of data of this kind when seeking the real cause of population limitation. Other examples which have already been considered in detail are the naïve deductions of many biologists that, because population densities often have a clear relation to the prevailing climate, therefore climate controls population densities, and the oversight by Gause of the essential space component of the Volterra equations which caused him to design inappropriate experiments to test the validity of these equations, and therefore to reach an erroneous conclusion.

Although the commonest source of error in population theory has been unjustifiable inference from often inappropriate data, it has occasionally been due to "theorizing" with little or no basis of ascertained fact. Thus Chapman based his well-known theory of population regulation wholly upon a supposed analogy between the resistance of environments to population growth, and the resistance of conductors to electric currents, as represented by Ohm's law. He brought forward no biological evidence, but contended that "the ratio of the number of organisms which should be present because of the inherent ability of organisms to reproduce themselves (the biotic potential) and the number which are present may be considered as the measure of the resistance of the environment" (Chapman 1931, p. 196). This analogy would be justifiable only if it were true that in a given environment density varied directly with "biotic potential", for the basis of Ohm's law is that electrical current in a given conductor varies directly with electrical potential. But this is not true, for it has already been shown that there is no constant relation between population density and "the inherent ability of organisms to reproduce", and that sometimes, notably in the experiments with *Lucilia* (see Fig. 2), there is an inverse relation between these quantities.

Thompson's mathematical investigations of the interaction of entomophagous parasites and their hosts (which he recapitulates in his 1939 article) are little better based. His primary assumption is not merely that each female parasite can lay a certain definite number of eggs, but that it does lay this number, so long as any hosts remain in the environment. It is not surprising, therefore, that he concludes that a parasite population can never overtake the host population (which is assumed to be free from any check other than the action of the parasites) unless its reproductive rate is greater than that of the hosts, and that in this situation the overtaking of the host population is inevitably followed immediately by the extermination of both hosts and parasites. These conclusions are clearly as unreal as is his primary postulate, which completely ignores the fact that the chance of a parasite finding sufficient hosts in which to lay its eggs must become small when the host density becomes very low.

It appears that Verhulst, Pearl, Lotka, Volterra, and Nicholson each independently chose the same factor as being of primary importance in population regulation, and Bailey based his mathematical investigation upon the postulates provided by Nicholson. This factor is the progressive decrease in the favourability of the environment which is associated with progressive increase in population density. Essentially the same simplifying assumptions were made by each of these investigators about the relation between such growth-opposing reaction and population density. Further postulates, implicit in the terms used, limit the application of the Verhulst-Pearl equations to competition of very simple microorganisms for favourable space, and the application of the Lotka-Volterra equations to simple microorganisms interacting as predators and prey. These limitations were not appreciated even by the authors themselves, and the attempt made by many biologists to use these equations to describe the growth and regulation of populations of higher animals has led to much misunderstanding.

A deplorable example of the misapplication of equations is the fitting of logistic curves to the data provided by growing populations of some of the higher animals. Thus Pearl (1926) succeeded in fitting logistic curves to growing populations of many different kinds. If he had claimed that the equations upon which these curves were based were merely convenient descriptions of the observed growth of the populations, one could not take exception to the procedure. Unfortunately, he went further and claimed that his success in curve-fitting showed "that populations grow in size according to the same mathematical law that individual animals and plants follow in the growth of their bodies in size" (Pearl 1926, p. 208). Examination shows that he did not hesitate to introduce new terms into his equations when they would not otherwise fit the data under examination. In this way he described the growth of the population of Sweden during the last 300 years by a logistic equation, in spite of the fact that during the period 1700 to about 1860 the percentage increase of the population per decade became progressively larger, in contrast to the characteristic progressive diminution with time of the rate of multiplication of cells in organisms, or of populations of microorganisms, to which the original logistic equation applied. Such curve fitting gives spurious relations.

The fact that the Nicholson-Bailey equations take into account the lag effects which are caused by the time taken by animals in development makes them applicable to certain of the higher animals, but their application was from the first explicitly restricted to predators of the entomophagous "parasite" type and their "hosts". Equations (**1**), (**2**), and (**3**) in the present article describe the equilibrium conditions for any kind of animal, and they can be modified by dividing the terms into their components to describe more precisely the equilibrium conditions for any particular kind of animal, as has been done for predators in equations (**4**) and (**5**). From these it is easy to derive equations describing growth and maintenance in populations of very simple microorganisms, as has been done in equations (**7**)-(**13**); but, because of development lag and the difficulties this introduces, such as complex changes in the age composition of populations, it is far more difficult to derive equations describing the growth and maintenance of populations of higher animals. Nicholson and Bailey (1935) have done so for the special case of predators which contest for their prey; but populations of animals which scramble for their governing requisites are far more difficult to represent mathematically.

Thus most of the well-known mathematical theories of population regulation are complementary, and each represents a different group of population systems. They fall quite naturally into the general scheme of classification developed in this article (see Fig. 6).

This brief review of population theories shows that much of the present confusion in the subject has been due to insufficient attention being given to the correct interpretation of data, and to a tendency to extend valid conclusions into fields in which the considerations upon which they were based do not apply. The question naturally arises as to whether or not this is also true of the present investigation.

(*c*) *Basis and Validity of Conclusions in Present Investigation*

In the following discussion the primary considerations upon which the present investigation was based are restated, and the validity of the conclusions reached is assessed.

All biologists are aware that populations are influenced by many and varied factors, but an underlying orderliness is equally evident. The necessary first step in the investigation, therefore, was to classify the various types of factors according to their influence upon populations, and to define and study those pertinent facts about animals and their populations which are axiomatic, or so well established by generations of observers as to be unquestionably true. Of these the following established facts seemed to me to be most significant and to provide the basis for an understanding of population dynamics:

(1) All animals have an innate ability to reproduce and to multiply under favourable conditions.

(2) The favourability or otherwise of the environment for a given species determines whether its population is permitted to grow or is caused to decrease.

(3) As every animal born must die, and can die only once, a population cannot persist for long periods in any given environment unless the birth-rate and death-rate are virtually equal (when each is averaged over a representative period); for if numbers of births and of deaths remained appreciably different the population would decrease or increase geometrically, so either directly falling to extinction, or causing its own extinction by overwhelming its environment, in a comparatively short time.

(4) As populations grow, the constituent animals use up more and more of the limited available quantities of depletable requisites (such as food and favourable space), and increasing density often intensifies the action of inimical factors (for example, by increasing the densities of any natural enemies dependent upon the animals concerned, or by increasing the concentration of harmful metabolites).

(5) Because animals produce such effects upon their environments, growing populations progressively reduce the favourability of some factors, whereas decreasing populations permit favourability to recover. Such compensatory reaction inevitably governs population densities at levels related to the properties of the animals and those of their environments.

(6) Consequently, when operating in association with density governing factors, non-reactive factors (such as climate) may have a profound influence upon density, for many non-reactive factors influence either the properties of animals or environmental favourability.

(7) Operating by themselves, however, non-reactive factors cannot determine population densities for, if sufficiently favourable, they permit indefinite multiplication or, if not, they cause populations to dwindle to extinction. On the other hand, they inevitably limit distribution to those areas within which they are favourable.

These basic considerations are of general application, being quite independent of the nature and of the complexity or otherwise of the situations in which the animals live. They are simply statements of well-established knowledge, and of implications which follow so directly from this knowledge as to be incontrovertible. It follows directly from these considerations that populations should exist in a state of balance in all favourable environments and that (except where some non-reactive factor causes the environment to be only barely favourable) density-controlled compensatory reaction enables populations to adjust themselves to severe external stresses, and so to remain in being. The observed facts that populations of the same species are maintained in many widely different environments without progressive change in density, and that they are not reduced to extinction when a new destructive factor is imposed, confirm these conclusions and show that balance cannot be due to a precise adjustment of the intrinsic properties of the animals to those of their environments.

After establishing these broad generalizations, further consideration showed that there are certain well-established facts which can be used to make other generalizations within more restricted fields. Density governing reaction is primarily dependent upon only two things—the characteristics of the population and those of its governing requisite, or group of requisites. All other pertinent factors produce their effects by modifying these characteristics. Analysis showed that requisites react upon population density in different ways according to whether they are favourable space, expendable things such as nonliving food, or other organisms used as food; and that four distinctive types of reaction by populations to changes in availability of governing requisites can be recognized. Different combinations of kinds of governing requisites and of kinds of population reaction thus constitute the 12 situations graphically shown in Figure 6. From knowledge of the characteristics of the animals and of their governing requisites, it was found possible to deduce the characteristic pattern of population growth and maintenance in each situation.

Although the facts upon which such generalizations were based have been well established by the experience of generations of biologists, no one would be content to accept the conclusions unreservedly without checking them by observation and experiment. All observations of natural populations and all experiments with laboratory populations known to me are consistent with the conclusions reached in this article, and many provide clear evidence supporting them—although it is true that the interpretations some investigators have placed upon their observations and experimental results are inconsistent with these conclusions. Most such observations and experiments have been inconclusive, for when investigators lack the guidance of a particular theory, it is almost inevitable that some observations having a crucial bearing upon that theory fail to be made, or to be recorded. Moreover, in order to check the correctness of a theory, it is not only necessary to find whether a population behaves in the way predicted, but also whether the underlying mechanism is that described by the theory. As already indicated, it is commonly difficult to identify mechanisms with certainty by field observation and, in general, little attempt has been made to analyse the influences of the different variables in the comparatively few laboratory populations that have been studied.

It was for this reason that an intensive study of laboratory populations of *Lucilia cuprina* was undertaken (Nicholson 1954). The pertinent results of some of these experiments have been briefly mentioned earlier in this article. In each experiment some one particular variable was singled out for study, the others being maintained constant—or the interaction of two, and sometimes three, variables was studied. Some biologists consider that the artificial conditions under which such populations are held make the results inapplicable to natural populations. This is untrue, for the factors studied are those known to influence natural populations, and an essential part of such experiments is the study of the interaction of such factors.

On the basis of the theory deduced from the general considerations already given, it was found possible to predict that *Lucilia* populations should behave in certain definite ways which should vary according to the particular conditions to which they are subjected. In all experiments the populations held under these defined conditions conformed to the predictions with gratifying precision, and the mechanism governing population growth and maintenance was revealed in detail and found to conform to that postulated. Not only did the results conform to the predictions made about animals which scramble for a consumable governing requisite (notably the maintenance by animals with a high birth-rate of violent and sustained periodic oscillations in density in a constant environment) but they also confirmed the general conclusions which it has been predicted should apply to any kind of population existing in a favourable environment. They clearly showed that populations limit themselves by progressively reducing the favourability of the environment as they grow, so maintaining themselves in a condition of balance with their environments; that on the average the number of births equals the number of deaths, imposed destruction not increasing mortality but merely causing a redistribution of mortality amongst the lethal factors; and that compensatory reaction enables them to accommodate themselves to even very severe environmental stresses.

(*d*) *Basis and Validity of Conclusions in Earlier Investigations by Nicholson and Bailey*

It is noteworthy that the investigations of Nicholson (1933) and of Nicholson and Bailey (1935), which dominantly dealt with the interaction of entomophagous parasites and their hosts (situation 3*c* in Fig. 6), apart from leading to special conclusions relating only to parasites and hosts (notably the production of oscillations in density which grow in amplitude with time), also led to the same general conclusions. This provides supplementary evidence about the soundness of these investigations, which were based upon considerations of well-established facts concerning factors known to influence natural populations of parasites and hosts. Until such time as they can be adequately checked by observation and experiment, the special conclusions reached can only be regarded as reasonable hypotheses, although they are far more soundly based than most opinions about the effects of interaction between entomophagous parasites and their hosts. Already there is much circumstantial evidence from field observations which supports some of these hypotheses. The experiment of de Bach and Smith (1941) in which pupae of *Musca domestica* were parasitized by *Mormoniella vitripennis* gives some support to the conclusion that interacting populations of hosts and parasites produce oscillations which grow in amplitude with time, although the experiment was unfortunately concluded before crucial results could be obtained. Probably the most important feature of this experiment is the close correspondence between the observed and the calculated densities of the hosts and parasites in each of the seven generations studied, which shows that with *Mormoniella,* at least, the postulate of random searching corresponds closely to the behaviour of the parasite.

Thompson (1939) bases most of his criticism of the investigations and conclusions of Nicholson (1933) and of Nicholson and Bailey (1935) upon his belief that this concept of random searching is unsound. Like Ullyett (1953) he places much stress upon the indisputable fact that individuals of many species search in ways which are far from random, but both authors ignore the statement of Nicholson (1933, p. 141) that "if individuals, or groups of individuals, search independently of one another, the searching within the *population* is unorganized, and therefore random. Systematic searching by individuals improves the efficiency of the individuals, but otherwise the character of the searching within a population remains unaltered." Only when the searching of individuals is systematically influenced by the activities of others does searching by the population as a whole become non-random, as when the individuals lay claim to territories. Consequently, random searching is a reasonable primary postulate when applied to entomophagous parasites. It should be noted that, in essentials, it is the same simplifying hypothesis as that used by Verhulst, Pearl, Lotka, and Volterra in their equations, which, stated in general terms, is that the chance of an individual obtaining a sufficient quantity of the governing requisite to enable it to produce one offspring varies directly with the density of the requisite at each given moment. This clearly is only a first approximation, but it must often be closely approached in fact. "Random searching" is simply a convenient term with which to refer to the underlying mechanism of this probability relation, at least with such animals as entomophagous parasites. It is interesting to note that Thompson (1924), following the example of Fiske (1910), used essentially the same probability relation when discussing the problem of superparasitism, but his unfortunate failure to use it also in his investigations of interaction between parasites and hosts made these quite unreal.

Both Thompson and Ullyett appear to hold the view that the conclusions of Nicholson and Bailey are completely dependent upon the assumption of random searching. This view is incorrect for, as has already been mentioned, even great departures from the condition of random searching may not prevent successive oscillations in density from growing in amplitude, as when the parasites are unable to search in a significant fraction of the environment. However, it is the part played by compensatory reaction to density change which these authors seem most loath to accept. The qualitative features of Nicholson and Bailey's conclusions concerning this are quite independent of the truth or otherwise of the concept of random searching. Without stating the precise relation between density and intensity of environmental reaction, essentially the same conclusions concerning the effects produced upon populations by density governed reaction to environmental change have been derived from the well-established fact that growing populations inevitably and progressively deplete some requisites, and they are confirmed by the experiments with *Lucilia* populations in which the relation between density and the success of the individuals is very different from that which is represented by the probability of random contacts. The concept of random searching applies only to certain kinds of animals; and, although it may represent part of the mechanism of compensatory reaction to density, it is not an essential part of this mechanism.

Ullyett (1953, p. 83) stated, "the possession of life endows the organism with one of its main characteristics, namely, that 'something extra' which is not found in inorganic nature." He also stresses the inherent plasticity of organisms, and the multiplicity of causes of mortality which even individually are not constants. He argued that because of these considerations mathematics is inherently inapplicable to the study of living organisms. This is a surprising claim when one considers the notable success of actuaries in dealing mathematically with the probability of events in human populations, events which are determined by a multiplicity of causes, including the plastic behaviour of man who is generally considered to possess "that something extra" in greater degree than any other organism. The mathematics used to describe populations always deals with the probability of certain occurrences amongst large numbers of individuals, and does not assume precise and invariable behaviour of the individuals. For the preliminary study of a problem it is often convenient to assume that particular properties or influences are constants, but this is not a necessary assumption. If it is known that these properties or influences vary in an orderly way, terms can be introduced to represent this particular orderliness; and it should be noted that even choice and free will in man are known to produce orderly influences upon events, provided the number of men exercising these abilities is very large.

(*e*) *The Collection and Interpretation of Evidence*: *Summary*

The foregoing considerations show clearly that, in order to obtain a knowledge of populations and of the mechanisms which regulate them, we must be prepared to use all means available to us for ascertaining and interpreting facts, for each has special virtues and limitations. Extensive observation has provided us with some general knowledge which has proved invaluable in enabling us to ascertain the general features and characteristics of populations. Intensive observation of particular populations provides us with special information about these populations, and enables us to determine in a general way what factors are influencing them—but commonly it is difficult to disentangle the influences of the individual factors. Laboratory experiment enables us to separate these factors physically and to determine their separate influences, and with further experiments we can determine the effects produced by these factors upon one another, so ultimately enabling us to interpret intelligently what we observe in the field.

Observations and experiments, however, do not themselves provide answers to our problems. It is necessary to devote at least as much care and energy to their design and interpretation as to the collection of data. The history of population investigations shows that their weakness has been mainly due to the inadequate use of rigorous thought; and the main source of error with theories and hypotheses has been a lack of a clear appreciation of the fact that conclusions reached can logically be applied only to situations which conform to the postulates upon which they were based.

Mathematics, being a particularly powerful tool of thought, should be employed wherever it is appropriate, but its limitations must be recognized. It is true that no equation could conceivably be produced which takes into account explicitly all factors known to influence populations; but this does not mean that mathematics is therefore useless when dealing with problems of natural populations, as some biologists appear to believe. However, there is no need to make equations as complex as this for, although the number of kinds of factors known to influence populations is very great, only a few of these significantly influence any given natural population. Moreover, it is often possible to represent the collective influence of a large number of factors by a single term, for in ultimate analysis all factors affect populations by influencing the birth-rate and longevity of the animals, or the availability and quality of the governing requisites, or the magnitude of the maintenance quanta of the governing requisites for the animals under the prevailing conditions. Consequently, knowing the kinds of effects the various factors produce upon the properties of the animals and those of their environment, it is possible to determine the kinds of effects which will be produced upon the population by any change in one or more of the factors by using relatively simple equations, as has been done earlier in this article. Mathematics thus provides a ready means of determining how populations may be influenced by given environmental conditions, which is generally all we want to know; but, if a truly quantitative representation of a population is required, a precise quantitative study of all the factors in the environment and of their individual influences upon the properties of the animals must necessarily be made.

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EXPERIMENTS ON THE RELATIVE ABUNDANCE OF TWO SIBLING SPECIES OF GRAIN WEEVILS

By L. C. Birch*

[*Manuscript received October* 30, 1953]

Summary

The small "strain" and the large "strain" of *Calandra oryzae* L. are sibling species. The small "strain" is common in stored wheat and rare in stored maize. The reverse is true for the large "strain." A series of four experiments showed how wheat favoured the small "strain" and how maize favoured the large "strain." Given a choice of wheat and maize the small "strain" and the large "strain" laid most of their eggs in wheat but the proportion was larger for the small "strain" as compared with the large "strain." When the insects were reared for several generations in wheat they laid more of their eggs in wheat. Likewise when reared in maize they laid more of their eggs in maize. But this "host conditioning" was not sufficient to prevent them from laying many eggs in the "wrong" grain. The innate capacity for increase of the small "strain" was greater than that of the large "strain" in wheat but in maize the large "strain" had a greater innate capacity for increase than the small "strain." In crowded cultures wheat again favoured the small "strain" by permitting greater maximum populations as compared with the large "strain." Maize favoured the large "strain" in this respect. When the two "strains" occurred together in crowded cultures one always drove the other out. The small "strain" was the successful one in wheat and the large "strain" was the successful one in maize. Although these four series of experiments illustrate ways in which wheat favours the small "strain" and maize favours the large "strain" they do not, in themselves alone, account for the segregation of the two "strains" in stored grain.

I. Introduction

The so-called small and large "strains" of the weevil *Calandra oryzae* L. do not interbreed and so are to be regarded as sibling species (Birch 1944). The two species differ in the mean size of individuals but there is a considerable overlap in size, the smallest of the large "strain" are the same size as the largest of the small "strain." Furthermore, with both "strains," the beetles reared from wheat are usually larger than those reared from maize (Birch 1946).

In Australia the small "strain" is common in stored wheat but it is so rare in maize that it has not yet been recorded from stored maize even though some careful searches have been made in South Australia, Queensland, New South Wales, and Western Australia. On the other hand the large "strain" is common in maize but it is so rare in wheat that it has not been recorded from stored wheat despite similar searches in several States. These differences in the distribution (or abundance) of the small and large "strains" are surprising, because both can be reared continuously in either wheat or maize in the laboratory.

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The possible causes of the difference in abundance of the two weevils in wheat and maize were investigated in a series of four experiments. These were done at a favourable temperature (29.1 ± 0.1°C) and relative humidity (70 per cent.).

Weevils were given a choice of wheat and maize in which to lay their eggs to see if they preferred one sort of grain to another (Section II). The weevils were reared separately in wheat and maize and records kept of the speed of development, duration of adult life, and the number of eggs laid throughout life. From the results of these experiments the innate capacity for increase was calculated (Section III). The two weevils were grown separately in crowded cultures in wheat and in maize to compare the relative rates of increase and the size of the populations when the quantity of food and the amount of space were kept constant (Section IV). They were also grown together in single containers in both wheat and in maize to find out the effect of one species on the numbers of the other (Section V).

II. Preference for Oviposition in Wheat or Maize

In each experiment eight pairs of newly emerged adult beetles were confined in small glass tubes containing 40 grains of wheat and 10 grains of maize. The total surface area of the wheat was about the same as the total surface area of the maize. The eggs are laid in the grain and were counted twice a week. Each time the eggs were counted the grain was discarded and replaced with fresh grain. The experiments were continued for 5 weeks and the results were expressed as the percentage of eggs laid in wheat per week.

Two series of experiments were done with each of the two "strains": in one the adults were obtained from cultures in which the weevils had been reared continuously in wheat for at least eight generations, in the other series the adults were from cultures in which weevils had been reared for a similar time in maize. Each experiment was replicated six times. The series was treated as one complex factorial experiment with two "strains" of weevil, two previous histories (reared in wheat or maize), five ages (0-1, 1-2, 2-3, 3-4, 4-5 wk), and six replicates.

The results are summarized in Table 1, which shows the total eggs laid per eight females and the percentage of these which were laid in grains of wheat from the second to the fifth week. From the second to the fifth week the total number of eggs laid each week did not vary much and it was appropriate to conduct an analysis of variance on percentages after they had been transformed to angles. The number of eggs laid in the first week was much smaller than in later weeks and so they could not be legitimately included in the analysis.

The percentage of eggs laid in wheat did not vary significantly from one week to the next and so we may simply compare the means for the four weeks, these are the four means in bold type in Table 1. The two "strains" laid most

Table 1

PERCENTAGE OF EGGS LAID BY THE SMALL AND THE LARGE "STRAINS" OF *C. ORYZAE* IN WHEAT WHEN GIVEN A CHOICE OF WHEAT AND MAIZE FOR OVIPOSITION

Temperature 29·1°C and relative humidity 70%. Each figure is the mean of six replicates

Previous History	"Strain"	Large					Small				
	Weeks	2	3	4	5	Mean	2	3	4	5	Mean
Reared in wheat	Percentage eggs laid in wheat	81·6	83·1	86·3	87·7	**84·7**	94·6	93·8	93·1	94·0	**93·9**
	Total eggs per 8 females in wheat and maize	187	244	257	266	239	275	276	246	209	251
Reared in maize	Percentage eggs laid in maize	76·6	75·1	74·0	62·2	**72·0**	88·6	89·8	91·0	85·9	**88·8**
	Total eggs per 8 females in wheat and maize	209	248	225	246	232	237	287	273	221	255

At $P = 0\cdot01$ significant difference of $\sin^{-1}\sqrt{x}/100 = 5\cdot34$ where x = percentage eggs laid in wheat.
Differences between "strains" are significant at $P > 0\cdot001$.
Differences between "histories" (reared in wheat or in maize) are significant at $P > 0\cdot001$.
Differences between ages are not significant at $P = 0\cdot01$.
None of the "interactions" was significant at $P = 0\cdot01$.

of their eggs in wheat, both when they had been reared for several generations in wheat and when they had been reared in maize. But the preference for wheat was reduced when the insects had been reared in maize, the reduction was 17 per cent. for the large "strain" and 5 per cent. for the small "strain." This indicates a certain amount of "host conditioning." The small "strain" laid a bigger proportion of its eggs in wheat than the large "strain." The largest difference in the percentage of eggs laid in wheat was between the small "strain" which had been reared in wheat (93.9 per cent.) and the large "strain" reared in maize (72 per cent.). This is a clear demonstration that the small "strain" reared in wheat laid very few of its eggs in maize; on the other hand, the large "strain" reared in maize laid 72 per cent. of its eggs in wheat. The experiments illustrate one way in which the small "strain" may be kept rare in maize, but they do not help us to understand how it is that the large "strain" is not common in wheat.

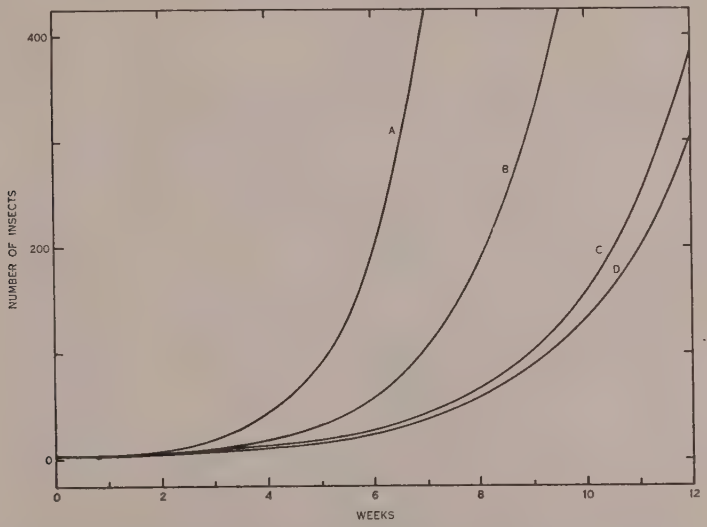

Fig. 1.—Theoretical geometric rate of increase of the small and large "strains" of *C. oryzae* in wheat and in maize at 29.1°C and 70 per cent. relative humidity. *A*, small "strain" in wheat ($\lambda = 2.15$). *B*, large "strain" in wheat ($\lambda = 1.76$). *C*, large "strain" in maize ($\lambda = 1.55$). *D*, small "strain" in maize ($\lambda = 1.52$). (λ is the finite rate of increase per female per week.)

III. INNATE CAPACITY FOR INCREASE

The innate capacity for increase of the two "strains" in wheat and in maize is summarized from Birch (1953*a*) in Table 2. The innate capacity for increase is the infinitesimal rate of increase of a population of stable age distribution. It is designated as r and is estimated from the survival rate at different ages and the fecundity rate at different ages (see Birch 1948). The second last

TABLE 2

INNATE CAPACITY FOR INCREASE OF THE SMALL AND LARGE "STRAINS" OF *C. ORYZAE* IN WHEAT AND IN MAIZE AT 29·1°C AND 70 PER CENT. RELATIVE HUMIDITY

"Strain"	Grain	Percentage Mortality of Immature Stages in Grain	Total Number of Eggs per Female	Duration of Development, Egg to Adult (wk)	Mean Length of a Generation	Rate of Multiplication per Generation	Mean Duration of Life of Adult Female (wk)	Innate Capacity for Increase (r)	Finite Rate of Increase per Female per Week (λ)
Small	Wheat	10	344	4·0	6·4	134·2	17·1	0·772	2·15
Small	Maize	13	70	5·0	8·2	30·5	23·2	0·417	1·52
Large	Wheat	10	208	4·4	8·0	89·4	18·1	0·564	1·76
Large	Maize	34·6	154	4·9	8·8	46·7	18·3	0·436	1·55

column in Table 2 gives values of r. The last column gives the finite rate of increase where $\lambda = e^r$ and is the finite rate of increase per female per week of a population of stable age distribution. In x weeks one pair would give rise to λ^x females and λ^x males. The theoretical curves of geometric increase derived from these relationships are shown for the four values of λ of Table 2 in Figure 1. In wheat the small "strain" has a much greater innate capacity for increase than the large "strain" (compare curves A and B). In maize the large "strain" has a slightly greater innate capacity for increase than the small "strain" (compare curves C and D). These differences in innate capacity are largely due to the differences in the total number of eggs laid by the two "strains" in wheat and in maize (column 4, Table 2).

The results demonstrate again the superiority of the small "strain" as compared with the large "strain" in wheat and the slight superiority of the large "strain" over the small "strain" in maize. But with both "strains" the innate capacity for increase was greatest in wheat.

Table 3

MAXIMUM NUMBERS OF ADULTS OF THE LARGE AND SMALL "STRAINS" OF *C. ORYZAE* IN WHEAT AND IN MAIZE WHEN POPULATIONS WERE GROWN IN 12 g OF GRAIN RENEWED AT REGULAR INTERVALS

Temperature 29·1°C and relative humidity 70 per cent. The figures shown are means of 15 replicates

Experiment	Mean Maximum Numbers of Adults	Mean Maximum Weight of Adults (g)
Large "strain" in wheat	600	0·98
Small "strain" in wheat	825	1·18
Large "strain" in maize	300	0·87
Small "strain" in maize	370	0·53

IV. Maximum Numbers when Food and Space were Limited

Birch (1953*b*) followed the trend in numbers of adults of the small and large "strains" in experiments in which a single pair of beetles was introduced into 12 g of grain. The grain was kept up to a total weight of 12 g by renewing it every 2 weeks. Experiments were done with both wheat and maize.

For the first 20-30 weeks the numbers increased, then followed long-term fluctuations which continued for the 2-3 years during which the experiments were continued. The full details of these experiments do not concern us here but only those aspects which have been abstracted in Table 3. This table shows the mean maximum number of adults in the fluctuations. The mean weight of these populations is also included in the table. The maxima rather than the means were compared because maxima have a reality in the population trends which the means do not possess.

In experiments in wheat the small "strain" reached the greatest numbers and the greatest weight; the populations of maximum size weighed 20 per cent. more than the populations of maximum size of the large "strain" in wheat. In maize the maximum numbers of the two "strains" were not very different, but because of their greater size the total weight of the large "strain" was 64 per cent. greater than the total weight of the biggest population of small "strain" in maize.

These experiments show that in crowded cultures both "strains" attain large numbers. In terms of the total weight of adults the small "strain" has much larger populations than the large "strain" in wheat. In maize the populations of the large "strain" weigh much more than those of the small "strain."

V. Effect of One Species on the Numbers of the Other when Crowded Together

Birch (1953*c*) grew the large and the small "strains" together in wheat and in maize. The experiments were similar to those reported in Section III except that a pair of both large and small "strains" were initially introduced into the 12 g of grain. In each of these experiments one species eventually became extinct. The successful species in each case was the one with the higher innate capacity for increase. When the two "strains" were grown together in wheat the large "strain" eventually became extinct. This took from 46 to 95 weeks, with a mean of 69 weeks for the 15 replicates. In maize the reverse result was obtained. The small "strain" became extinct in each of the 15 replicates although it took from 74 to 150 weeks (mean = 100 weeks) for this to happen.

These experiments demonstrate quite clearly (since the replicates in any one series all gave the same result) that when the two "strains" come together in crowded cultures wheat favours the small "strain" and maize favours the large "strain."

VI. Conclusion

The four series of experiments (Sections II-V) show four ways in which wheat favours the small "strain" as compared with maize and how maize favours the large "strain" as compared with wheat. But all four ways combined could not in themselves account for the absence of the large "strain" from stored wheat and the absence of the small "strain" from stored maize. The experiments showed that when adults were confined in a small space with both wheat and maize both "strains" laid their eggs in both sorts of grain, though mostly in wheat. Only a small proportion of the eggs of the small "strain" were laid in maize. On the other hand, a quite large proportion of the eggs of the large "strain" were laid in maize as well as in wheat. The innate capacity for increase of the small "strain" was greater than that of the large "strain" in wheat. In maize the innate capacity of the large "strain" was greater than that of the small "strain." A greater innate capacity for increase enables the insect to take advantage of a favourable period for increasing its numbers to a greater extent than would otherwise be possible. The differences in innate capacity for increase were reflected in the maximum weight of the populations attained in crowded cultures; again the small "strain" exceeded the large in wheat and the large "strain" exceeded the small "strain" in maize. When crowded together the large "strain" became extinct in wheat and the small "strain" became extinct in maize. But even in the severe conditions of these experiments this took a year or more to happen. If both species happened to infest stored grain we might expect to find both "strains" together, even when crowded, at least at some stages of the infestation, because of the long time it takes for one to eliminate the other.

At the most we can say that these are four ways which would tend to cause the small "strain" to be more common in wheat than in maize and vice versa for the large "strain." They could not in themselves account for the absence of the small "strain" from stored maize and the absence of the large "strain" from stored wheat. Nor is this surprising since these experiments were done at one constant temperature and at one constant relative humidity and with relatively small quantities of grain. Although the two "strains" lay their eggs in both wheat and maize when confined in a small space with both grains it is quite possible that they do not do this in the field where grain is not mixed up in this way, and where they are free to wander large distances. A store of maize may not be attractive to the small "strain" and a store of wheat may not be attractive to the large "strain." Crombie (1941) showed that the grain borer *Rhizopertha dominica* was attracted to a particular sort of food by smell. Once within range of the "right" smell the act of oviposition was dependent upon the "right" tactile stimulus. Not all objects were equally effective in inducing oviposition, those with rough surfaces or crevices had more eggs laid on them than smooth objects. It is possible that in the field smell guides the small "strain" of *C. oryzae* to alight on wheat rather than maize and vice versa for the large "strain." This is not known. But the chance of maize being infested by the large "strain" before the small "strain" is increased by the greater tendency of the large "strain" to fly and infest cobs of corn on the growing crop. So far as I know there are no records of wheat having been infested in the standing crop by the small "strain."

VII. Acknowledgments

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ECDYSIS IN THE ISOPOD *PORCELLIO SCABER* (LATREILLE)

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Summary

The outside layers of specimens of the isopod *Porcellio scaber* (Latreille) were examined at various times during the moult cycle, using transverse sections of the whole animal. Several structures associated with the cuticular layers were noted to alter over this period. The epidermal cells are active and vacuolated during the ecdysal phase but are inactive and at times non-vacuolated during that of the intermoult. The new epicuticle appears before the endocuticle and is apparent at least 21 hr prior to moulting. About 5 hr after moulting, the new chitinous cuticle is differentiated into exocuticle and endocuticle; the deposition of these components of the cuticle being due to the progressive solidification of a secretion of the epidermal cells. By using the criteria set out in this paper, an individual's position in its moult cycle can be estimated.

I. Introduction

The volume of literature dealing with the structure and methods of formation of the arthropod cuticle is considerable. Little investigation has been made of the times at which changes occur, or of cellular and other changes which could serve to identify an individual as being in one part or other of the ecdysal cycle. This work was undertaken to discover whether cellular and other activity could be so correlated. Such a measure is required as a preliminary to an investigation of age grouping in the Arthropoda.

II. Materials and Methods

(*a*) *Material*

Investigations were carried out on the isopod *Porcellio scaber* (Latreille) since this was easily cultured and readily available. Gorvett's procedure for culturing the animals (Gorvett 1946) was followed and the use of potato in the culture proved just as satisfactory as carrot. Females with young in the brood pouches and immature animals were not used; mature males and non-breeding females were examined without distinction.

(*b*) *Method*

(i) *Time Sequences.*—The integument of *P. scaber* is not cast in one piece, but in two. The integument of the "posterior portion," consisting of the abdo-

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men and the last three thoracic segments, is shed before that of the rest of the body—the "anterior portion." Using the instant of the initial detachment from the old cuticle as datum, the times at which various relevant observable changes occurred during moulting of the posterior and anterior portions of *P. scaber* are given in Tables 1 and 3 respectively, the animals being nominated by the letters at the head of the respective columns.

TABLE 1

OBSERVED TIME LAPSES OF VARIOUS CHARACTERISTICS RELATED TO THE MOULTING OF THE POSTERIOR PORTION OF *PORCELLIO SCABER* AFTER COMMENCEMENT OF MOULT

Characteristic Observed	Time Lapse for Each Specimen (min)				
	O*	M†	J†	N†	H†
Uropod beneath 6th thoracic tergite	5				
Uropod beneath 5th thoracic tergite	10				
Uropods free of old cuticle, i.e. duration of ecdysis	15	15	20	20	20
Contractions ceased	60	45			35
Legs flexing	65	50		65	
Commenced eating cuticle	120	80	80	120	80
Ceased eating cuticle		140	140		
Time to consume cuticle		60	60		

*Times accurate to nearest minute.
†Times accurate to ±3 min.

The time taken to complete the withdrawal of the posterior portion from the respective cuticles was 15-20 min after the initial freeing of the uropods. Likewise the time of complete withdrawal of the anterior portion, following on the initial freeing of the head, was from 10 to 21 min. Muscular contractions which accompany these withdrawals commence before, assist during, and continue for 20-40 min after shedding these old cuticles. For the purpose of this paper, the duration of moult is regarded as the time interval between datum and the complete withdrawal of the head or abdomen from their respective cast cuticles. The time lapse between the posterior moult and the anterior moult is referred to as the *intramoult* period, and the lapse between two consecutive renewals of the complete integument as the *intermoult* period. The intramoult period in our specimens was 17-24 hr, as recorded in Table 2. Gorvett (1946) stated the intermoult period to be 2-3 months for *P. scaber*. This period was not ascertained for our specimens. In these, however, it was possible to obtain both a premoult and a postmoult condition in a single individual, because of the time lapse between moulting of the posterior and anterior portions. By killing and fixing animals at a known interval after the posterior portion has moulted, timed pre- and postmoult sections were obtained. One individual was used for each set of observations.

(ii) *Histological Technique.*—Specimens were fixed in Carnoy for 12-24 hr and then brought to 65 per cent. alcohol and treated with "Diaphanol." Methyl salicylate was the intermediate clearing agent, followed by benzene at reduced pressure. A vacuum embedding technique was employed before the final embedding. Sections were cut at 7-8 μ and a Mallory one-step triple stain was used for the initial identification of structure; later sections were examined, unstained, with a Zeiss positive phase-contrast microscope.

TABLE 2

PORCELLIO SCABER: TIMES OF INTRAMOULT PERIODS

Animal	Time* (hr)
O	24
M	23½
N	22½
H	21½
J	20
No. 8	17

*These times are accurate to ±15 min.

TABLE 3

OBSERVED TIME LAPSES OF VARIOUS CHARACTERISTICS RELATED TO THE MOULTING OF THE ANTERIOR PORTION OF *PORCELLIO SCABER* AFTER COMMENCEMENT OF MOULT

Characteristic Observed	Time Lapse for Each Specimen (min)				
	H*	N*	J†	M†	O†
Head beneath 1st thoracic tergite	3	2			
Head beneath 2nd thoracic tergite	8	3	5		
Head beneath 3rd thoracic tergite	10	5			
Head beneath 4th thoracic tergite	12	6			
Head free of old cuticle, i.e. duration of ecdysis	21	12	20	10	15
Antennae folded		15	20	10	20
Antennae straight		21	30	20	30
Contractions ceased		36	60	30	50

*Times accurate to nearest minute.

†Times accurate to ±2 min.

III. TERMINOLOGY AND CUTICLE STRUCTURE

The exoskeleton of *P. scaber* is composed of three layers; an outer non-chitinous layer, the epicuticle; and two inner chitinous layers, the outer of

TABLE 4

CUTICULAR AND SUBCUTICULAR CHANGES IN RELATION TO PREMOULT, MOULT, AND POSTMOULT CONDITIONS OF *PORCELLIO SCABER*

Criteria	Intermoult (21+)	Premoult (Hr before moult)						At Moult (0 hr)	Postmoult (Hr after moult)								Intermoult (120+)
		21	20	19	17	11	2		1	3	5	7	11	20	21	120	
Epidermal cell size	A	B	B	B	B	C	C	C	C	C	B	B	A	A	A	A	A
Epidermal vacuoles	?	?	D	?	D	E	F	F	F	F	F	F	F	?	?	?	?
Secretion beneath cuticle	?	G	G	G	G	G	H	H	H	H	H	?	H	H	H	?	?
New epicuticle		p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	
New cuticle	L v.s.	?	?	?	?	?	J	J	J	J	K	K v.s.	K v.s.	L v.s.	L v.s.	L v.s.	L v.s.
Old cuticle		L v.s.	L v.s.	L v.s.	L v.s.	L	K										
Old epicuticle	—	p	p	p	p	p	p										

See Figures 1-4 for explanation of lettering. v.s. = Vertical striations; ? = criteria not apparent; p = epicuticle present.

which is the exocuticle, and the inner is the endocuticle. These layers were identified and named according to the terminology of the decapod cuticle developed by Drach (1939).

Vertical striae were not seen in the homogeneous epicuticle, but they were clearly defined in the endocuticle. These striae may have obscured horizontal laminations which were only rarely seen. The thickness of the chitinized layers varies in different animals and in different regions of the same animal. Beneath the exoskeleton lies a cellular layer, the epidermis, which also varies in size. Subjacent to this is a thin basement membrane. In the general interstitium beneath the epidermis, tegumental glands were seen. Rosette glands in the head region and lobed glands in the lateral tergites, as described by Gorvett (1946), were present.

IV. Choice of Criteria of Ecdysal Activity

From the examination of sections of animals, at various times in the growth cycle, changes in a number of structures were evident, as follows:

(*a*) Volume of the epidermal cells.
(*b*) The size of the vacuoles in the epidermal cell.
(*c*) The quantity of secretion beneath the cuticle.
(*d*) The presence or absence of new epicuticle.
(*e*) The thickness of new and old cuticles.

These criteria were grouped into several major categories (Figs. 1-4; Plate 1) for the better tracing of changes throughout the cycle. The size of the epidermal cell nucleus was not found to vary to any marked extent during the intramoult period in *P. scaber*. This is in agreement with the position existing in the isopod *Asellus aquaticus* Linnaeus, as Needham (1946) recorded the absence of mitotic division in the epidermis during this period in that species. Accordingly the nucleus size at the intramoult was taken as the standard for the estimation of the above changes. The following criteria were developed in the course of the study:

Epidermal cells whose nuclei almost filled the cells are designated “small.” “Medium” and “large” cells are arbitrary grades made to include cells whose volume was considerably more than the volume of the nucleus. These relationships are shown photographically in Plate 1, Figure 1, and diagramatically in Figure 1. The terms “small,” “medium,” and “large” are again used when grading the vacuole sizes in these cells (Fig. 2; Plate 1, Fig. 2). Where no vacuoles were apparent in the epidermal cells, the condition is indicated by a question mark in Figure 6. When secreted material was present between the cuticle and epidermis; where a thin film of secretion was seen, either on the inside of the cuticle or on the outside of the epidermis, it is said to be “small”; if the secretion filled the space between cuticle and epidermis, then it is regarded as “large” (Fig. 3; Plate 1, Fig. 3). Where no secretion was apparent, the condition is indicated by a question mark in Figure 7.

The division of the cuticle into three groups is made, depending on the total thickness of the cuticle, and on the components of that cuticle in relation to nucleus sizes of the associated epidermal cells. A thin homogenous endocuticle, as found in newly moulted animals, is considered "small" and a thicker cuticle, consisting of a thin exocuticle and thin endocuticle, "medium." A "large" cuticle is composed of a relatively thick endocuticle as compared with the exocuticle, which was roughly the same as that found in the "medium" cuticle (Fig. 4; Plate 1, Fig. 4).

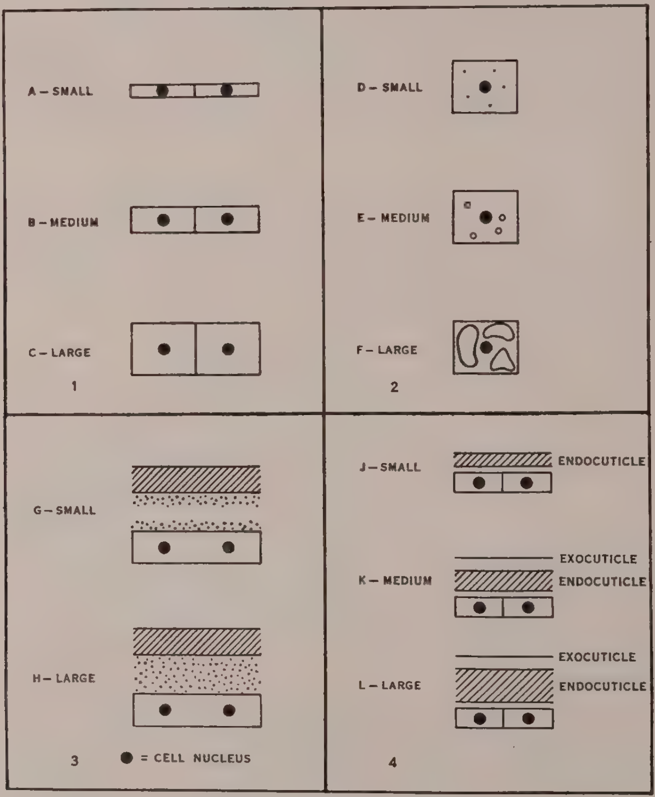
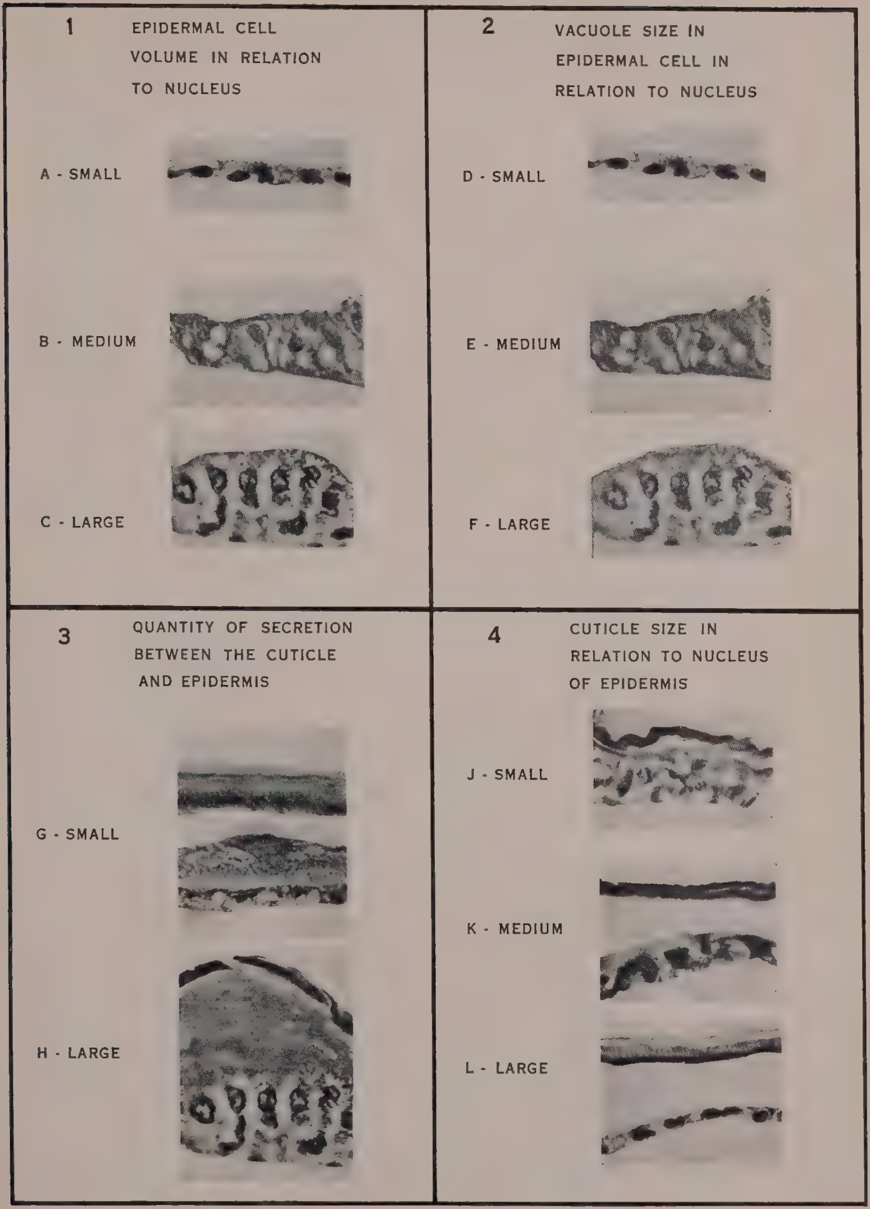


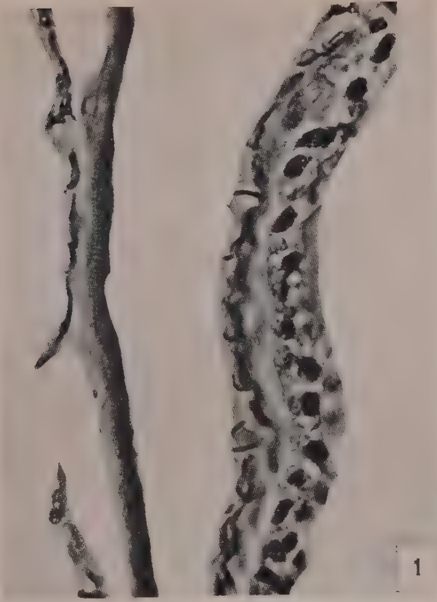
Fig. 1.—Epidermal cell volume in relation to nucleus.
Fig. 2.—Vacuole size in epidermal cell in relation to nucleus.
Fig. 3.—Quantity of secretion between the cuticle and epidermis.
Fig. 4.—Cuticle size in relation to nucleus of epidermis.

V. Results

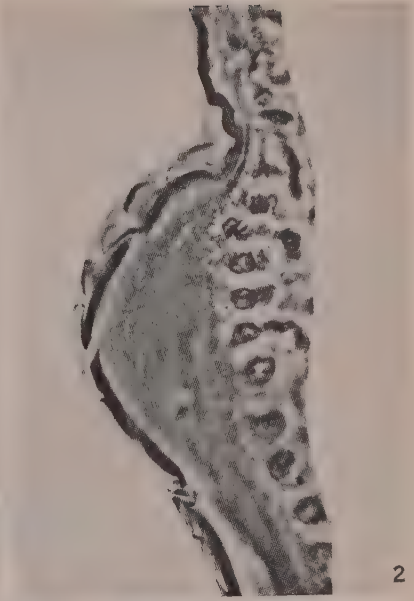
The observed structural changes during the intramoult period are set out in Table 4, using the lettering applied to the criteria schematized in Figures 1-4. The following descriptions extend the observations summarized in Table 4, which is a composite table, relating the various criteria to the time of ecdysis

ECDYSIS IN *PORCELLIO SCABER*


1
EPIDERMAL CELL VOLUME IN RELATION TO NUCLEUS
A - SMALL
B - MEDIUM
C - LARGE
2
VACUOLE SIZE IN EPIDERMAL CELL IN RELATION TO NUCLEUS
D - SMALL
E - MEDIUM
F - LARGE
3
QUANTITY OF SECRETION BETWEEN THE CUTICLE AND EPIDERMIS
G - SMALL
H - LARGE
4
CUTICLE SIZE IN RELATION TO NUCLEUS OF EPIDERMIS
J - SMALL
K - MEDIUM
L - LARGE



1



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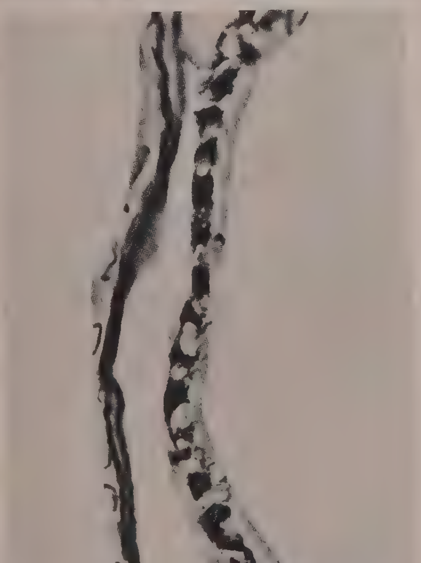

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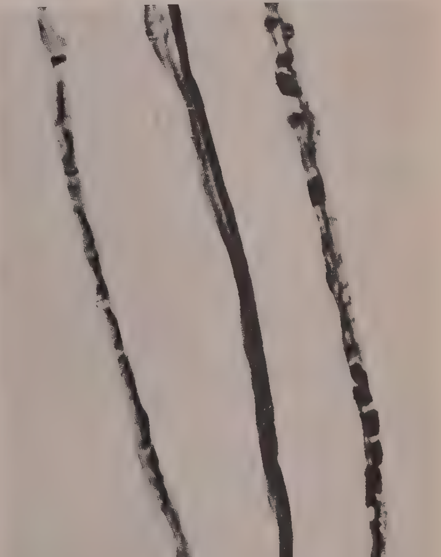


4

as datum, irrespective of which portion of the animal is moulting. Consequently, the indicated times are approximations only.

(*a*) *Specimens, One Each at* 21, 20, 19, *and* 17 *hr Premoult*

The epidermis was of medium size and contained small or no vacuoles. A thin layer of secretion was present beneath the new cuticle of which only the epicuticle was apparent. The old cuticle was thick and vertically striated. In one specimen the old cuticle was pitted on the under side.

(*b*) *Specimen at* 11 *hr Premoult* (*Plate* 2, *Fig.* 1)

The epidermal cells were large, containing medium-sized vacuoles. Of the cuticle, only the epicuticle was present, and beneath this a small layer of secretion was observed. A thick, old cuticle existed but its vertical striations were not distinct.

(*c*) *Specimen at* 2 *hr Premoult*

The space between the new cuticle and the epidermis was filled with secretion, and both the epidermal cells and their contained vacuoles were maximum in size. The new homogeneous endocuticle and the new epicuticle were present. The old cuticle was reduced in size and had diffuse vertical striations. The old epicuticle invariably accompanied the old cuticle.

(*d*) *Specimen at Moult* (*Plate* 2, *Fig.* 2)

The conditions of the structures found at moulting, and for 3 hr after moulting, simulated those of the 2-hr premoult animal except that in the two former the old cuticle was absent.

(*e*) *Specimens, One Each at* 5 *and* 7 *hr Postmoult* (*Plate* 2, *Fig.* 3)

The epidermal cells were smaller and their vacuoles still large. These cells were overlain by a thick layer of secretion filling the subcuticular space. The new cuticle was differentiated into exo- and endocuticles, the latter possessing faint vertical striations; the exocuticle was homogeneous and remained so until the cuticle was cast.

(*f*) *Specimen at* 11 *hr Postmoult*

The epidermal cells were small, and apart from this change the remaining criteria were similar to those found in the 5- and 7-hr-postmoult conditions.

(*g*) *Specimens, One Each at* 20 *and* 21 *hr Postmoult*

No vacuoles were seen in the small epidermal cells and the secretion filled the space beneath the thick vertically striated endocuticle.

(*h*) *Specimen at* 120 *hr Postmoult* (*Plate* 2, *Fig.* 4)

The structures 120 hr after moulting were almost identical with those found in intermoult animals. No vacuoles were present in the small epidermis and no secretion was observed beneath the fully formed thick cuticle. The epicuticle and exocuticle were homogeneous and the endocuticle possessed distinct vertical striations.

The changes which occurred in four of the criteria, i.e. epidermal cell size, vacuole size, quantity of secretion, and cuticle size; at premoult, and on to postmoult, were plotted against time (Figs. 5-8).

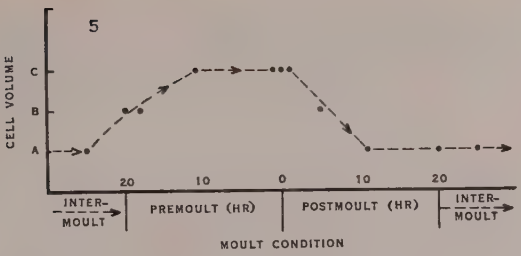
Two animals which were about to shed the posterior portions of their cuticles were, for some reason, unable to complete this process even after a lapse of 13 hr. Sections of one of these animals showed two fully formed cuticles surrounding the posterior portion of the body. The old endocuticle was thicker and more distinctly striated than the new endocuticle, and beneath this new cuticle was a thick layer of secretion. Both the new and old epicuticles were clearly seen.

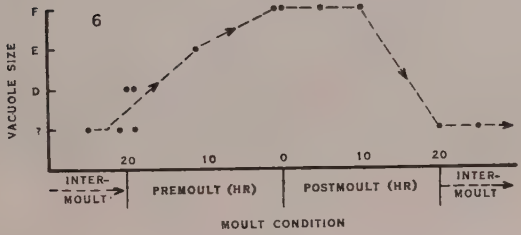
VI. Discussion

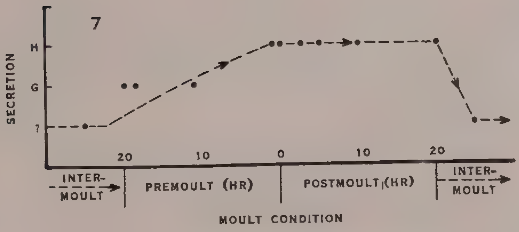
The activity of epidermal cells, vacuoles, and epidermal secretions follows a similar cycle during moulting in these specimens (Figs. 5-7). Needham (1946) also found a simple inflation of epidermal cells and increased vacuolation at moult for *Asellus aquaticus*. He and other workers on crustacean cuticle (Yonge 1932; Drach 1939; Dennell 1947*b*; Gorvett 1946) stated that the epidermis actively participated in the formation of new cuticle.

Since a large amount of secretion is present during the deposition of the endocuticle and no secretion is evident in the intermoult period (Table 4), it is here suggested that the cuticle of *P. scaber* is formed by the progressive solidification of a secretion produced by the epidermal cells. Once produced, this substance remains outside the epidermis and gradually forms the new chitin layers, independent of the later activity of the epidermal cells. This view was not upheld by Wigglesworth (1948) (Insecta) or by Yonge (1932) (Crustacea : Decapoda), who believed that chitin layers are formed by modification of the upper portion of the epidermal cells. Dennell (1947*a*), however, found that some insects do secrete a substance which forms a new integument, and Clausen and Richards (1951) also considered the possibility that this secretory method of cuticle formation occurred rather than that of epidermal cell modification.

The epicuticle of *P. scaber* in our specimens was produced before the endocuticle and appeared at least 21 hr before moult. It was not observed to increase in size and was quite homogeneous. The results of Yonge's investigation on *Homarus vulgarus* (1932) are contrary to these observations, as he found that the epicuticle appeared after the endocuticle and increased in size during the intermoult period. Gorvett (1946) found that the epicuticle of *P. scaber* formed after the endocuticle and assumed the source of this cuticle layer to be the rosette glands because of the correlation between the cyclical activity of these glands and moulting. Drach's results on *Maia squinando* Herbst (Drach 1939), regarding the time of epicuticle deposition, agree with those expressed in this paper, i.e. that the epicuticle is developed before the endocuticle.







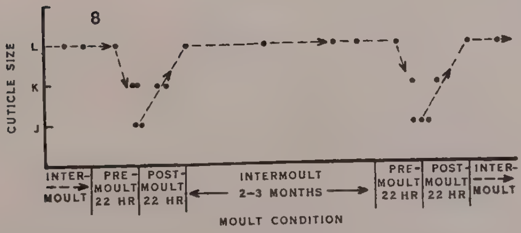


Fig. 5.—Cell volume in relation to moult condition (key in Fig. 1).

Fig. 6.—Vacuole size in relation to moult condition (key in Fig. 2).

Fig. 7.—Quantity of secretion in relation to moult condition (key in Fig. 3).

Fig. 8.—Cuticle size in relation to moult condition (key in Fig. 4).

The decrease in thickness and the increase in diffuseness of the vertical striations of the endocuticle before the initiation of ecdysis suggested that this layer was being dissolved and possibly resorbed. Yonge (1932) believed that invading cells dissolved the cuticle, as he often observed the nuclei of these cells in cuticle indentations. Although no nuclei were seen in *P. scaber*, the endocuticle of one premoult animal was pitted.

In *Homarus vulgarus*, Yonge (1932) suggested that an indication of the moult state is given by the size of the gastroliths. Work done by one of us (K.S., unpublished data) indicates that this is not reliable for the commercial Western Australian marine crayfish, *Panulirus longipes* (M.-E.). Moult conditions in the isopod *P. scaber* can be estimated using the criteria set out in this paper as a guide, and a preliminary investigation suggests that they are also applicable to the above decapod species. Consequently, since a close estimate of the position of an individual with relation to its position in the moult cycle is a necessity in the study of the biology and technology of that valuable commercial species, this work will be extended to cover species such as *Panulirus longipes* in detail.

VII. Acknowledgments

This work was carried out in the Zoology Department, University of Western Australia. The advice of members of that Department is acknowledged. Thanks are also due to Mr. E. Walsh, Zoology Department, University of Western Australia, for the processing of the photomicrographs, and to the Technical Section, Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W., for the final preparation of the figures.

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Yonge, C. M. (1932).—On nature and permeability of chitin. *Proc. Roy. Soc.* B **111**: 298.

Explanation of Plates 1 and 2

Photomicrographs of unstained sections of cuticle of *P. scaber* cut at 7-8 μ using a phase-contrast microscope, a mercury vapour lamp, and a No. 11 Wratten green filter with an 8-sec exposure on Ilford Microneg (Panchromatic) film. The magnification of *all* photographs in Plate 1 is × 370, in Plate 2 × 440.

Plate 1

Selected photographs from various slide preparations of *P. scaber* representing actual differences in the criteria chosen. These may be directly compared with the diagrammatic representation in Figures 1-4.

Fig. 1.—Epidermal cell volume in relation to nucleus.
Fig. 2.—Vacuole size in epidermal cell in relation to nucleus.
Fig. 3.—Quantity of secretion between cuticle and epidermis.
Fig. 4.—Cuticle size in relation to nucleus of epidermis.

Plate 2

Fig. 1.—Eleven hr premoult. Note the old epicuticle and cuticle on the left, also the new epicuticle and "medium"-sized epidermis on the right.

Fig. 2.—The condition at moult. Note the new epicuticle on the extreme left and new endocuticle present as a dark line, the secretion beneath this, and the "large" epidermal cells.

Fig. 3.—Five hr postmoult. Note the differentiation into exocuticle and endocuticle. The epidermal cells have decreased in size.

Fig. 4.—One hundred and twenty hr postmoult. Note the epicuticle, fully formed exocuticle and endocuticle, and the thin layer of "small" epidermal cells.

THE AUSTRALIAN ARMYWORMS OF THE GENUS *PERSECTANIA* (LEPIDOPTERA : NOCTUIDAE)

By I. F. B. Common*

[*Manuscript received August* 11, 1953]

Summary

Persectania ewingii (Westwood) is one of the more important armyworms in southern Australia and Tasmania. Conflicting information about its ecology in Tasmania and Western Australia has led to a critical examination of the identity of specimens referred to this species from various parts of its reputed range. It is shown that a second species, *P. dyscrita*, sp. nov., which is apparently restricted to areas of southern Australia with a low summer rainfall, has previously been confused with *P. ewingii*. In New Zealand, a third distinct species, *P. aversa* (Walker), has been misidentified as *P. ewingii*. *P. ewingii* and *P. dyscrita* are confined to Australia, and *P. aversa* to New Zealand. The male and female genitalia of the three species are figured and a key to the two Australian species is provided.

Introduction

One of the more important Australian armyworms is *Persectania ewingii* (Westwood), which has been reported as a pest of pastures and cereal crops in many parts of southern Australia, including Tasmania. Evans (1943) stated that two generations were completed each year in Tasmania, serious damage occurring during December and January in barley, oats, wheat, flax, and pea crops, as well as in pastures. In the 1950-51 outbreak reported by Miller, Kjar, and Martyn (1951), oat crops suffered most severely whereas wheat was not seriously attacked. Newman (1927), on the other hand, in outlining the habits of an armyworm referred to as *P. ewingii* in Western Australia, stated that the larvae showed a strong preference for wheat and often would not touch oats. It was mainly a pest of the wheat areas and was seldom of importance in the coastal and southern districts that received a higher rainfall. In the inland wheat areas the pupae formed in the spring did not produce adults until the following autumn rains, and the larvae caused their greatest damage in August and September.

The present study was undertaken to determine whether these conflicting observations were due to a confusion of more than one species under the name of *P. ewingii*. Series of specimens from Tasmania, the type locality of this species, have been compared with specimens from the mainland and from New Zealand, where it is also reputed to occur.

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The material examined came from the collections of the Queensland Museum, Brisbane; The Australian Museum and The Department of Agriculture, Sydney; The National Museum of Victoria and the Department of Agriculture, Melbourne; The Tasmanian Department of Agriculture, Hobart; The South Australian Museum and The Waite Agricultural Research Institute, Adelaide; The Western Australian Department of Agriculture, Perth; and the Division of Entomology Museum, C.S.I.R.O., Canberra. New Zealand specimens were provided by the Cawthron Institute, Nelson.

Genus PERSECTANIA Hampson

Persectania Hampson, 1905, Catalogue of the Lepidoptera Phalaenae in the British Museum **5**: 386.

Type species: *Noctua* (*Xylophasia* ?) *ewingii* Westwood, 1837.

Proboscis fully developed; labial palpi curved obliquely upwards, apical segment porrect; frons smooth, rounded; scales on frons and vertex roughened, forming rounded prominence on frons; antennae in male fasciculate-ciliated, in female with very short pubescence and bristles, eyes hairy. Thorax with tegulae forming a transverse dorsal ridge, prominent medial divided crest on prothorax and a less prominent medial spreading crest on metathorax. Abdomen with dorsal crest of scales on basal segment and lateral tufts of hair.

Male genitalia with diffuse corona of stout spines and a marginal series of shorter incurved spines on the cucullus of the valve; aedeagus with bunch of 3 or 4 straight cornuti. Female genitalia with bursa copulatrix a simple large sac without signa, with ductus seminalis arising directly from the wall of the bursa copulatrix.

Hampson erected the genus *Persectania* to contain 4 Australian and New Zealand species distinguished by the form of the frons from *Sideridis* Hübner, *Leucania* Ochsenheimer, and *Cirphis* Walker. Meyrick (1912) also distinguished *Persectania* from *Leucania* and *Aletia* Hübner by the frons, and regarded *Cirphis* and *Sideridis* as synonyms of *Aletia*. Turner (1920) could not recognize any differences between the frons of *Persectania ewingii* and that of *loreyi* Duponchel and *abdominalis* Walker placed by Hampson in the genus *Cirphis*. He therefore included these 3 species, together with a series of other Australian species, in the genus *Sideridis* which, like Hampson, he used in preference to *Aletia*. The combination *Sideridis ewingii* has thus frequently been used in the Australian economic literature.

Franclemont (1951) made an important contribution to a rational understanding of the Hadeninae by attempting to stabilize the generic names of some of the armyworms. He emphasized the value of characters provided by the male and female genitalia in delimiting genera. *Persectania* and certain related genera he considered to be a primitive element of a group of genera, including *Aletia*, in which the cucullus of the male valve bears a diffuse corona of large stout spines. In the genera related to *Leucania*, on the other hand, the cucullus of the valve lacks a corona.

The form of the male and female genitalia of *Persectania ewingii* appears to justify the separation of this and related species from *Aletia* and other armyworm genera represented in Australia, including *Eurypsyche* Butler, *Hypopteridia* Warren, *Dasygaster* Guenée, *Cirphis* Walker, and *Leucania* Ochsenheimer. Much more revisionary work is necessary, however, before the classification of the Australian Hadeninae is placed on a sound basis.

Two names, *Noctua* (*Xylophasia* ?) *ewingii* Westwood and *Chloantha composita* Guenée, have previously been proposed for Australian species now referred to the genus *Persectania*. Tasmania is the type locality of both these species. The latter was placed in the synonymy of *P. ewingii* by Hampson (1905). Westwood's types are preserved in the Hope Department of the Oxford University and in the British Museum, but the type of *ewingii* has not so far been found in either of these institutions and is probably lost. The female lectotype of *Chloantha composita* is in the Muséum National d'Histoire naturelle, Paris, and the genitalia have been dissected by P. E. Viette. All the Tasmanian specimens examined in the course of this study have female genitalia essentially similar to the lectotype of *composita*. These specimens also correspond to Westwood's figure of *ewingii*. It has therefore been concluded that both names refer to the 1 species. As *ewingii* antedates *composita*, the latter is correctly placed in the synonomy of *ewingii*. The male genitalia are similar to those of the Tasmanian specimen figured by Franclemont (1951).

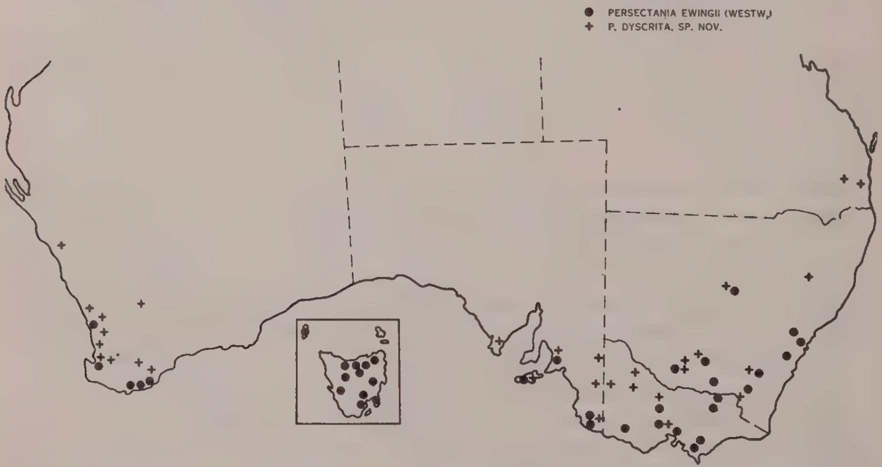

Fig. 1.—Distribution of *Persectania ewingii* (Westw.) and *P. dyscrita*, sp. nov. in Australia based on adult records.

Specimens hitherto regarded as *P. ewingii* from New Zealand have been compared with Tasmanian specimens, and the genitalia, particularly of the female, show the New Zealand species to be distinct. It is concluded therefore that Franclemont (1951) was in error in figuring the female genitalia of a specimen from New Zealand as *P. ewingii*. For the New Zealand species, the name *P. aversa* (Walker) (1856, List Spec. Lep. Ins. Brit. Mus. 9: 113) should be employed. *Mamestra maori* Felder, *Morrisonia peracuta* Morrison, and *Leucania dentigera* Butler are probably synonyms of *P. aversa*.

The examination of series of collected specimens and those reared by the author, in one instance through 4 generations, has shown that a second, apparently unnamed, species occurs on the Australian continent. This species was probably responsible for the armyworm outbreaks reported by Newman (1927) in the Western Australian wheat belt. Although *P. ewingii* occurs in the coastal areas of south-west Australia from Perth to Albany, no specimens have been seen from the wheat belt (Fig. 1). While rearing this species and *P. ewingii* under similar conditions in a heated insectary, there was evidence that the former was able to aestivate for several weeks as a prepupa.

At present it seems desirable to restrict the genus *Persectania* to the 2 Australian and the single New Zealand species. This is suggested especially by the form of the female genitalia, which provide some of the most reliable characters for delimiting genera in the Hadeninae.

Key to Australian Species of the Genus Persectania

Hind wings above fuscous, only slightly lighter in basal ½; male genitalia with clavus prominent, rounded; female genitalia with ductus seminalis leaving bursa copulatrix at anterior end . . . . *P. ewingii* (Westw.)

Hind wings above with terminal ½ fuscous, basal ½ whitish; male genitalia with clavus produced into bilobed process with narrow neck; female genitalia with ductus seminalis leaving bursa copulatrix at posterior end . . . . *P. dyscrita,* sp. nov.

Description of Species

Persectania ewingii (Westwood)

Fig. 2*A-D*; Plate 1, Figs. 1-3

Noctua (*Xylophasia* ?) *ewingii* Westwood, 1839, Trans. Ent. Soc. Lond **2** (Proc.): lv, pl. 20, fig. 1.

Chloantha composita Guenée, 1852, Hist. Nat. Ins., Spec. Gén. Lépid., vi, Noctuelites **2**: 114 (type locality: Tasmania).

Persectania evingi (Westwood) Hampson, 1905, Cat. Lep. Phalaenae Brit. Mus. **5**: 386.

Sideridis ewingii (Westwood) Turner, 1920, Trans. Roy. Soc. S. Aust. **44**: 137.

Male

Head and labial palpi with projecting scales grey, tinged with brown; frons with transverse black bar; crown dark brown. Thorax grey, tinged with olive-ochreous and dark brown; tegulae with median transverse black line, narrowly edged with white above; patagia with broad upper and lower edge of dark brown, and with series of black scales near upper edge; under side of thorax with long purplish grey hairs; legs grey, tinged with dark brown and purplish, distal 3 segments of fore tarsi black, middle and hind tarsi fuscous distally. Abdomen grey, becoming darker posteriorly, lateral tufts dull purplish grey, anal tuft dull purplish brown with some orange scales on valve; purplish grey beneath with sublateral line of black spots. Fore wing light grey, heavily suffused in most specimens with fuscous and olive-ochreous or ferruginous; 2 black longitudinal streaks towards base, one below cell and another near dorsum; the veins near outer and lower ½ of cell outlined with black; sub-basal line represented

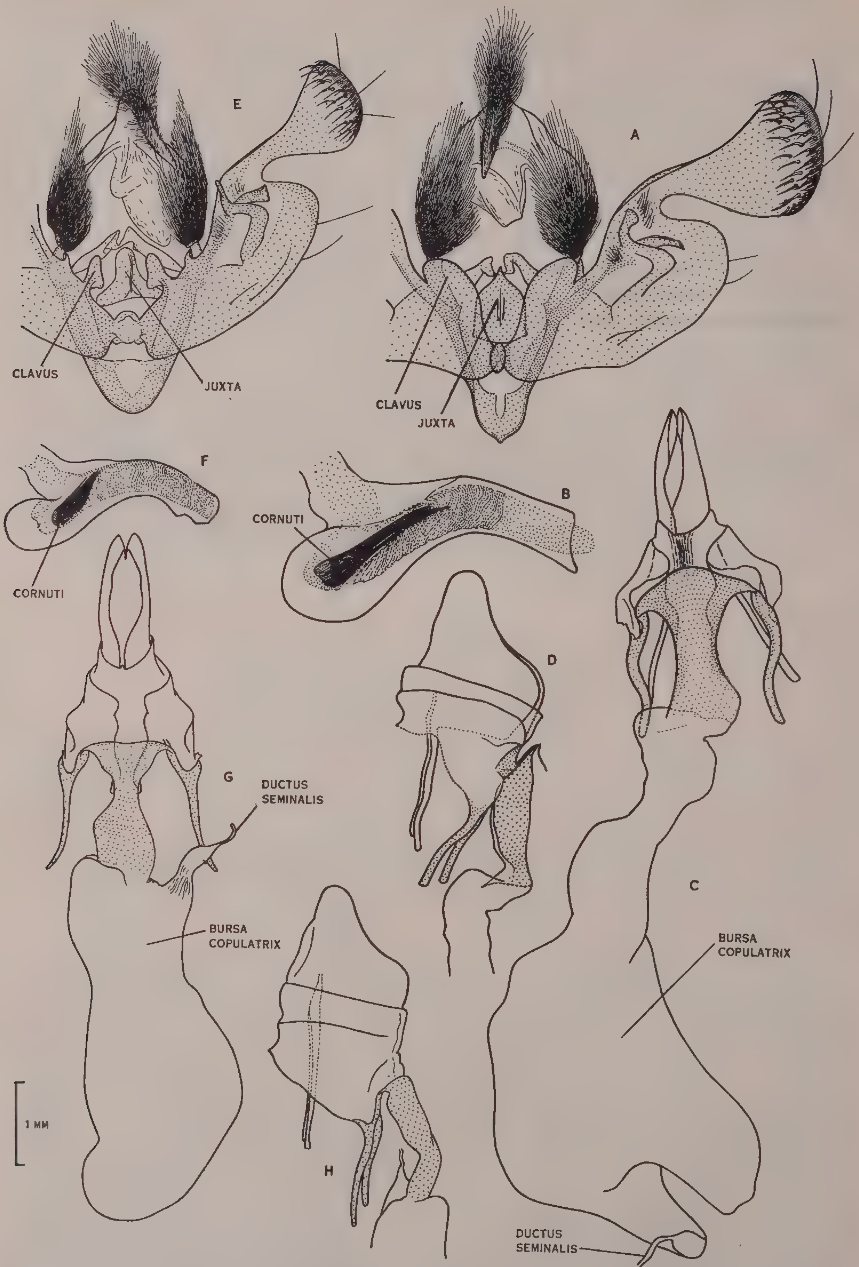

Fig. 2.—Genitalia of Australian species of *Persectania*. *A, B, P. ewingii* (Westw.), male, Scottsdale, Tas., 26.ii.1927, G. F. Hill. *C, D, P. ewingii* (Westw.), female, Cressy, Tas., 12.xi.1952, I. F. B. Common. *E, F, P. dyscrita,* sp. nov., holotype male. *G, H, P. dyscrita,* sp. nov., allotype female. (Camera lucida.)

by a short, outwardly oblique fuscous line from costa near base; antemedial line indistinct, with large dentations; postmedial line from just beyond ½ costa, bent outwards to R_4 just below 4/5 costa, thence very strongly dentate to just beyond ½ dorsum; subterminal line black, from apex obliquely inwards to below M_2, then with 2 strong outward dentations reaching termen on M_3 and Cu_1 and another on Cu_2; area between postmedial and subterminal lines paler and area beyond subterminal line darker than remainder of wing; orbicular and reniform whitish, defined by black, the former elongate and in most specimens confluent with the latter; a series of black dots on termen between veins. Hind wing fuscous, slightly paler in basal half; cilia white with fuscous sub-basal line. Under side light grey irrorated with fuscous and tinged with purplish; cell of fore wing and area beyond suffused with fuscous, terminal row of black dots between veins; hind wing with black discoidal spot and broad black terminal fascia from apex to below Cu_2, the tornus irrorated with fuscous.

Female

Similar to male but with ground colour of thorax and fore wing silvery grey, usually without olive-ochreous suffusion. Purplish grey tinge of abdomen and under side of wings greatly reduced and usually absent.

Genitalia

Male: Costa gently curved, clavus prominent, rounded, juxta with nearly parallel sides, tapering abruptly to point above; vesica with bunch of cornuti about ½ as long as aedeagus.

Female: Bursa copulatrix without signum, narrowed towards ductus bursa, broad anteriorly with sac-like recess on right side; ductus seminalis from anterior end of bursa copulatrix.

Expanse

Male: Mean 40.4 mm (range 30.0-45.0).
Female: Mean 43.6 mm (range 38.8-48.4).

Type locality: Terra van Diemenii (Tasmania).

Type: The type is presumably lost, since it is in neither the Oxford University Museum nor the British Museum (Natural History).

Specimens examined: 79 ♂ ♂, 128 ♀ ♀.

NEW SOUTH WALES: Adaminaby, 20, 23.x.1918, 1 ♂, 2 ♀ ♀ (C.S.I.R.O.); 19.x.1918, 1 ♀ (Qld. Mus.). Albury, 18.ix.1952, I. F. B. Common, 2 ♀ ♀ (C.S.I.R.O.). Croydon Park, 1.x.1909, 1 ♀ (Aust. Mus.). 13 Miles E. of Deniliquin, 3.x.1952, I. F. B. Common, 1 ♂, 1 ♀ (reared from pupae, larvae in swarms) (C.S.I.R.O.). Gordon, 15.ix.1948, A. Musgrave (Aust. Mus.). Mt. Irvine, 21.ii.1944, P. Messmer, 1 ♂ (reared) (Aust. Mus.). Manly, 28.x.1905, 1 ♀; 5, 12.xi.1905, 2 ♀ ♀; 14.x.1906, 1 ♀; 6.xi.1906, 1 ♀; 11.x.1924, 1 ♀ (all Aust. Mus.). Mittagong, 12-16.xi.1924, 1 ♂, 1 ♀ (Aust. Mus.). 9 Miles E. of Narrandera, 2.x.1952, I. F. B. Common, 1 ♀ (C.S.I.R.O.). Sydney, 30.x.1897, 1 ♂ (S. Aust. Mus.); Oct. 1913, 1 ♂ (Aust. Mus.). Trangie, 17.x.1952, B. Cameron, 1 ♀; 1-18.xi.1952, B. Cameron, 1 ♂, 3 ♀ ♀ (all C.S.I.R.O.).

AUSTRALIAN CAPITAL TERRITORY: Black Mountain, Mar. 1930, 1 ♂, 1 ♀; Apr. 1930, W. Rafferty, 1 ♀; 18, 19.vi.1950, 19.i.1951, 27.iii.1951, 27-29.x.1951, 29.iii.1952, 21.iv.1952, 28.ix.1952, 16-31.x.1952, 1-3.xi.1952, 4.xii.1952, 2-18.iii.1953, 16.v.1953, 25.iv.1953, I. F. B. Common, 15 ♂ ♂, 16 ♀ ♀ (all light trap) (all C.S.I.R.O.). Mt. Gingera, 5800 ft., 15.x.1952, I. F. B. Common, 1 ♀ (C.S.I.R.O.). Mt. Ginini, 5100 ft., 15.x.1952, I. F. B. Common, 1 ♂ (C.S.I.R.O.).

VICTORIA: 2 ♀ ♀ (Qld. Mus.). Black Rock, Feb. 1903, 1 ♂, 1 ♀ (Nat. Mus.). Bogong High Plain, June 1951, L. J. Clarke, 1 ♀ (C.S.I.R.O.). Castlemaine, 16.iii.1907, W. E. Drake, 1 ♂ (Nat. Mus.). Dunkeld, 13.xii.1921, 1 ♂ (C.S.I.R.O.). Fish Creek, Dec. 1952, 2 ♂ ♂, 4 ♀ ♀, T. Hogan (C.S.I.R.O.). Gisborne, 16.iii.1897, 1 ♀; Apr. 1897, 1 ♀; 2.x.1902, 1 ♂; 21.x.1902, 1 ♂; 4.xi.1902, 1 ♀ (all Nat. Mus.); 9.iii.1910, G. Lyell, 1 ♀ (Aust. Mus.); 10.xi.1916, G. Lyell, 1 ♀; 20.x.1918, 1 ♂; 8, 9.xii.1918, G. Lyell, 2 ♀ ♀; 5, 13.x.1919, G. Lyell, 1 ♂, 1 ♀; 15.iii.1920, G. Lyell, 1 ♀; 30.x.1923, G. Lyell, 2 ♂ ♂; 18.ix.1928, 1 ♂; 17.xi.1928, 1 ♀ (all Nat. Mus.). Leongatha, 26.ii.1930, G. F. Hill, 2 ♀ ♀ (bred) (C.S.I.R.O.). Melbourne, 26.ix.1927, G. F. Hill, 1 ♂ (C.S.I.R.O.); 18.ix.1947, A.B., 1 ♂ (Nat. Mus.). Moe, 7-19.iv.1931, 1 ♂ (Nat. Mus.); 19.ii.1933, 1 ♂ (C.S.I.R.O.).

TASMANIA: 1 ♂, 1 ♀ (Qld. Mus.); 17.x.1950, E. J. Martyn, 1 ♀ (Tas. Dep. Agric.). Castra, 11.xi.1952, I. F. B. Common, 1 ♀ (C.S.I.R.O.). Cradle Mt., 3000 ft, 6.ii.1934, 1 ♂ (C.S.I.R.O.). Cressy, 12.xi.1952, I. F. B. Common, 1 ♀ (Fig. 2*C*, *D*) (C.S.I.R.O.). Deloraine, 12.xi.1952, I. F. B. Common, 1 ♀ (C.S.I.R.O.). Devonport, 5, 9.iii.1941, J. W. Evans, 2 ♂ ♂ (Tas. Dep. Agric.). Dilston, 21.x.1952, E. J. Martyn, 2 ♀ ♀ (in flight) (Tas. Dep. Agric.). Hobart, Lea, 1 ♀ (C.S.I.R.O.); 14.x.1916, G. H. Hardy, 1 ♀ (Aust. Mus.); 2.ix.1951, L. W. Miller, 1 ♀; 20-22.x.1952 and 2.xi.1952, E. J. Martyn, 5 ♀ ♀ (light trap) (all Tas. Dep. Agric.). Huonville, 24, 26.ii.1941, J. W. Evans, 2 ♂ ♂ (reared ex armyworms); 2-9.iii.1941, J. W. Evans, 1 ♂, 4 ♀ ♀ (reared ex armyworms) (all Tas. Dep. Agric.). Kindred, 13.x.1952, E. J. Martyn, 2 ♂ ♂, 2 ♀ ♀ (in flight) (Tas. Dep. Agric.). King I., 24.x.1952, E. J. Martyn, 2 ♂ ♂, 3 ♀ ♀ (Tas. Dep. Agric.). Launceston, 1 ♀ (Qld. Mus.); 2 ♂ ♂, 2 ♀ ♀ (S. Aust. Mus.). Port Arthur, 7.iii.1928, G. F. Hill, 1 ♀ (reared) (C.S.I.R.O.). Ridgeway, 12-17.v.1948 and 27.x.1948, C. Oke, 4 ♂ ♂, 6 ♀ ♀ (Nat. Mus.). Ross, 12.xi.1952, I. F. B. Common, 1 ♀ (C.S.I.R.O.). Scottsdale, 22-26.ii.1927, G. F. Hill, 3 ♂ ♂ (reared) (Fig. 2*A*, *B*) (C.S.I.R.O.). Snug R., Mar. 1927 and Mar. 1928, Ian Harman, 1 ♂, 1 ♀ (Nat. Mus.). Spreyton, 27.x.1952, E. J. Martyn, 1 ♂, 1 ♀ (Tas. Dep. Agric.). Strahan, 20.x.1899, 1 ♀ (Tas. Dep. Agric.).

SOUTH AUSTRALIA: Adelaide, Mar. 1930, W. K. Hughes, 1 ♂ (C.S.I.R.O.); Nov.-Dec. 1934, D.C.S., 1 ♂ (larvae attacking cereals); 15.viii.1945, 1 ♂ (reared from pupa in grass pots in glass-house) (both Waite Inst.). Blackwood, 24.iii.1949, R. Underdown, 1 ♂ (C.S.I.R.O.). Kangaroo I., A. M. Lea, 1 ♂ (S. Aust. Mus.). Mingbool, 7.xii.1944, J.D. and H.G.A., 1 ♀ (reared from armyworm in swarm on flax stubble); 13.iii.1949, 1 ♂ (reared from larva) (both Waite Inst.). Mt. Gambier, E. Guest, 1 ♂; 8.iv.1945, 1 ♂ (reared from larva attacking grass) (Waite Inst.). Parkside, 2 ♀ ♀ (S. Aust. Mus.). Taratap, 5.xi.1952, N. B. Tindale, 1 ♂ (reared, larvae in plague numbers) (S. Aust. Mus.).

WESTERN AUSTRALIA: 1 ♀ (W.A. Dep. Agric.). Albany, 5.x.1951, I. F. B. Common, 1 ♂, 3 ♀ ♀ (C.S.I.R.O.). Busselton, 25-28.x.1920, 1 ♀ (Aust. Mus.); 1.ix.1948, W. M. O'Donnell, 2 ♀ ♀ (W.A. Dep. Agric.). Crawley, 6.xi.1934, K. R. Norris, 1 ♀ (C.S.I.R.O.). King George Sound, 1 ♀ (Aust. Mus.). Lennox, 7.ix.1928 and 4.viii.1929, 2 ♀ ♀ (Nat. Mus.). 10 miles W. of Nornalup, 3.x.1951, I. F. B. Common, 2 ♀ ♀ (C.S.I.R.O.). Perth, 20-25.ix.1951, I. F. B. Common, 8 ♀ ♀ (C.S.I.R.O.); 2.x.1951, J. A. Mahon, 1 ♀ (C.S.I.R.O.); 29.xi.1951, I. F. B. Common, 4 ♂ ♂, 5 ♀ ♀ (reared from eggs from ♀ ♀ in light trap) (C.S.I.R.O.); 21.iv.1952, I. F. B. Common, 2 ♂ ♂ (F_4 generation from eggs from ♀ ♀ in light trap) (C.S.I.R.O.). Scarborough, 22.ix.1951, I. F. B. Common, 1 ♀ (C.S.I.R.O.). Youngs Siding, 27.xi.1950, 1 ♂, 1 ♀ (attacking ryegrass) (W.A. Dep. Agric.).

Comments

Hampson (1905) gave the date of Westwood's description of *Noctua* (*Xylophasia* ?) *ewingii* as 1837. However, Musgrave (1930) indicated that the actual date of publication was 1839. His conclusion was based on the dates of publication of the Transactions of the Entomological Society of London given by Wheeler (1912). Although Westwood's description was read for the meeting of June 5, 1837, it was published with the plate on July 1, 1839 (A. Musgrave, personal communication).

The distribution of *P. ewingii* appears to be limited mainly to the southern half of Australia, where the larvae are normally grass feeders (Fig. 1). Superficially it resembles the New Zealand species *P. aversa* (Walker), which has previously been placed in the synonymy of *P. ewingii.* However, the terminal fascia on the under side of the hind wings is poorly defined in *aversa* and is represented in most specimens by a fuscous irroration. A series of black terminal dots are clearly visible on the under side of the hind wings, but in *ewingii* these dots are obscured by the black terminal fascia. The genitalia of the males are rather similar, but may be distinguished by the more strongly curved costa of the valve in *aversa* (Fig. 3*A*). The clavus is more prominent in *ewingii* and the juxta tapers abruptly to a point whereas in *aversa* it tapers more gradually. The female genitalia are readily distinguished. In *ewingii* the ductus seminalis leaves the bursa copulatrix at its anterior end, but in *aversa* (Fig. 3*D*) it leaves the bursa near the middle.

The female genitalia of the lectotype of *composita* have a very small projection from the wall of the bursa copulatrix near the posterior end. The other specimens examined are without this process, though otherwise closely similar, and there is little doubt that it is aberrant.

Westwood's original description of *Noctua* (*Xylophasia* ?) *ewingii* appeared as a footnote to an account of the gregarious habits of the larvae by Ewing (1839). Apart from the outbreaks in Tasmania referred to by Miller, Kjar, and Martyn (1951), several serious outbreaks occurred in 1952 both on the mainland and in Tasmania. Annual winter grasses, including *Hordeum leporinum* Link. (barley grass) were destroyed over extensive areas of the Riverina, N.S.W., particularly near Deniliquin and Berrigan in August. The moths emerged in early October and were collected very abundantly in mercury vapour light traps at Canberra, reaching a maximum in late October and early November. Larval outbreaks followed in southern Victoria and in Tasmania in December, and may have been due to large-scale migrations of the moths from farther north. Both *P. ewingii* and *Pseudaletia australis* Franclemont were responsible for the Victorian outbreaks. It is probable that the extensive outbreaks in South Australia in the late winter were also due to *P. ewingii* (H. Lower, personal communication).

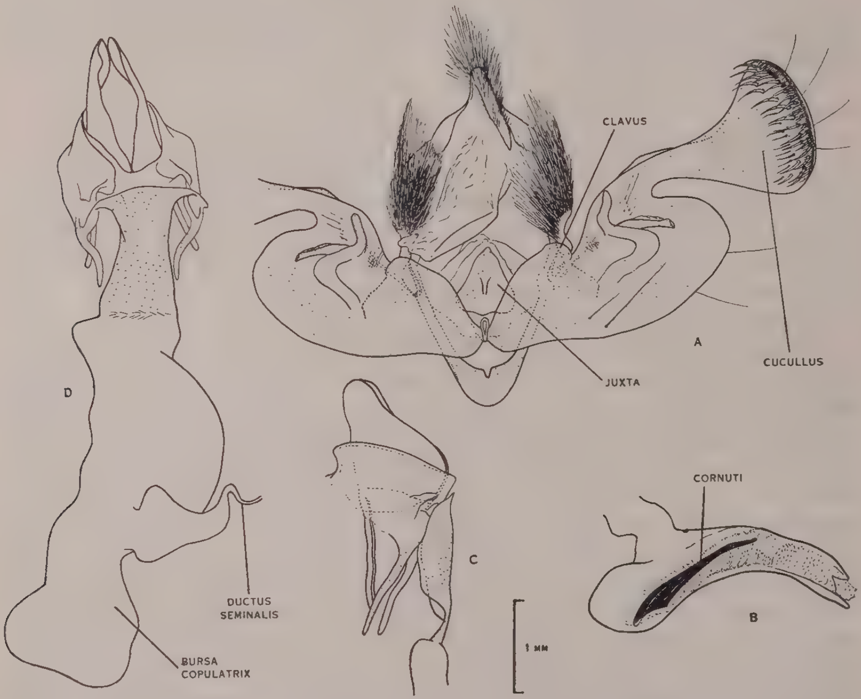

Fig. 3.—Genitalia of *Persectania aversa* (Walk.). *A, B,* male, Taumeranui, N.Z., 15.x.1939 (light trap) (C.S.I.R.O.). *C, D,* female, New Zealand, 20.v.1941 (C.S.I.R.O.). (Camera lucida.)

Persectania dyscrita,* sp. nov.

Fig. 2*E-H*; Plate 1, Figs. 4-6

Holotype male: Black Mountain, Canberra, A.C.T., 31.x.1952, I. F. B. Common (light trap); allotype female: Black Mountain, A.C.T., 3.xi.1952, I. F. B. Common (light trap); paratypes: a series of 19 specimens of both sexes from the same locality.

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*δύσκριτος = hard to determine.

Holotype male

Head grey, irrorated with dark grey, palpi whitish irrorated with fuscous on outside of 2nd segment, frons with dull fuscous transverse bar. Thorax dull ochreous-grey, tegulae with black transverse line, patagia with lower edge dark grey and with oblique black line near upper edge; under side of thorax with long grey hairs; legs grey, distal 3 segments of fore tarsi dull black. Abdomen grey above, white beneath with sublateral line of black spots. Fore wing dull grey suffused with dull ochreous-brown within and below cell; a longitudinal black streak just below cell in basal 1/3 of wing and a 2nd similar streak sometimes present just above dorsum; sub-basal line represented by very short oblique ill-defined line from costa near base; antemedial line very indistinct, represented by a fuscous strigule on costa just before ¼ and a line with 2 large dentations on fold and near dorsum; postmedial line black from beyond ½ costa, bent outwards to R_4 just below 4/5 costa, thence strongly dentate on veins to 2/3 dorsum; black subterminal line from apex obliquely inwards to below M_2, then with 2 strong outward dentations reaching termen on M_3 and Cu_1 and another on Cu_2; area between postmedial and subterminal lines light grey with ochreous suffusion, beyond subterminal line dark grey with ochreous suffusion; a series of black dots on termen between veins; orbicular and reniform ochreous-grey outlined with black, reniform with some white scales, orbicular oval, separate from reniform (but in odd specimens confluent). Hind wing light grey basally with broad ill-defined fuscous marginal fascia; cilia white, ochreous towards base. Under side, fore wings light grey, with fuscous subterminal suffusion beyond cell, series of black dots on termen between veins; hind wings white, with very slight fuscous irroration on costa, slight discoidal spot, and broad black terminal fascia from apex to Cu_2, tornus white. Expanse 40.0 mm.

Allotype female

Similar to male. Expanse 45.0 mm.

Genitalia

Holotype male: Costa gently to strongly curved, clavus produced into a bilobed process with narrow neck; juxta broad at base, becoming rapidly narrower towards upper end, sides concave; vesica with bunch of cornuti about 1/3 as long as aedeagus.

Allotype female: Bursa copulatrix without signum, sides nearly parallel, ductus seminalis from posterior end of bursa copulatrix.

Expanse (type series)

Male: 37.8 mm (range 34.0-40.4).
Female: 40.1 mm (range 33.6-45.6).

Type locality: Black Mountain, Canberra, A.C.T.

Types: The holotype male and allotype female, together with 11 paratypes, are in the Division of Entomology Museum, C.S.I.R.O., Canberra. Two paratypes, a male and a female, have been deposited in each of the following museums: the British Museum (Natural History), the Australian Museum, Sydney, the South Australian Museum, Adelaide, and the National Museum of Victoria, Melbourne.

Specimens examined: 51 ♂♂, 65 ♀♀.

QUEENSLAND: Brisbane, 10.x.?, J.A.K., 1 ♂ (Nat. Mus.). Toowoomba, 4.x.1924, 1 ♂ (Qld. Mus.).

NEW SOUTH WALES: 6 miles E. of Finley, 18.ix.1952, I. F. B. Common, 1 ♂ (C.S.I.R.O.). Gin Gin, 21.x.1952, L. Chinnick, 1 ♀ (light trap); 8-10.x.1952, L. Chinnick, 1 ♂ (light trap) (both C.S.I.R.O.). Jerilderie, 9, 10.xi.1923, J. Cattanach, 1 ♂, 1 ♀ (reared) (N.S.W. Dep. Agric.). Mt. Kosciusko, 5000 ft, 23.i.1914, 1 ♂ (C.S.I.R.O.). Murrurundi, 29.x.1933, 1 ♂ (Qld. Mus.). Yanco, 26.ix,6.x.1932, K. C. McKeown, 2 ♀♀ (Aust. Mus.). Trangie, 14, 31.x.1952, B. Cameron, 2 ♂♂ (light trap); 18.xi.1952, B. Cameron, 1 ♀ (light trap); 24.iv.1953, B. Cameron, 1 ♀ (light trap) (all C.S.I.R.O.).

AUSTRALIAN CAPITAL TERRITORY: Black Mountain, 31.x.1952, I. F. B. Common, 2 ♂♂, 1 ♀ (holotype and 2 paratypes); 3.xi.1952, I. F. B. Common, 1 ♂, 1 ♀ (allotype and paratype); 25.ix.1952, 5.xi.1952, 25.xi.1952, 4.xii.1952, 8.ii.1953, 24.ii.1953, 1.iii.1953, 24.iii.1953, 1.iv.1953, 23.iv.1953, and 25.iv.1953, I. F. B. Common, 5 ♂♂, 10 ♀♀ (all light trap; paratypes); 11.i.1953, I. F. B. Common, 1 ♀ (reared from eggs from ♀ in light trap; paratype) (distributed as indicated above).

VICTORIA: Bendigo, 2.x.1921, 1 ♂ (Aust. Mus.). Birchip, 1 ♀ (Nat. Mus.). Daytrap, 8.xii.1917, 1 ♀ (Nat. Mus.). Gisborne, 21.xi.1909, G. Lyell, 1 ♂ (Nat. Mus.). Kiata, 14.xi.1945, A.B., 1 ♀ (Nat. Mus.). Williamstown, 1 ♂ (Qld. Mus.).

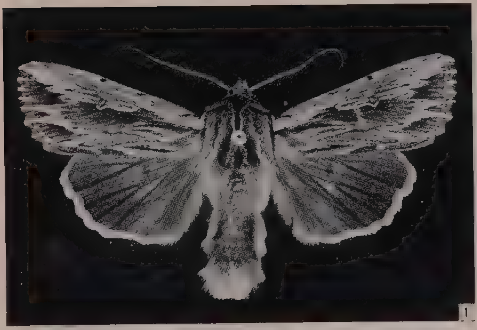
SOUTH AUSTRALIA: Adelaide, A. M. Lea, 1 ♀; Oct. 1919, N. B. Tindale, 1 ♀ (both S. Aust. Mus.). Bordertown, A. M. Lea, 2 ♂♂, 4 ♀♀ (S. Aust. Mus.). Kingscote, Kangaroo I., 24.xi.1945, 3 ♂♂, 1 ♀ (C.S.I.R.O.). Mt. Gambier, E. Guest, 1 ♂ (S. Aust. Mus.). Parkside, 1 ♀ (S. Aust. Mus.). Pinnaroo, 4 ♀♀ (Coll. Lower) (S. Aust. Mus.). Port Lincoln, Lea, 1 ♂ (S. Aust. Mus.).

WESTERN AUSTRALIA: Armadale, 12.v.1934, K. R. Norris, 1 ♀ (C.S.I.R.O.). Beverley, F. H. du Boulay, 1 ♂ (S. Aust. Mus.). 16 miles S. of Borden, 9.x.1951, I. F. B. Common, 3 ♂♂ (C.S.I.R.O.). Busselton, 25-28.x.1920, 1 ♀ (Aust. Mus.); 1.ix.1949, W. M. O'Donnell, 1 ♀ (W.A. Dep. Agric.). Collie, Cardiff, 28.x.1927, 1 ♀ (Nat. Mus.). Katanning, 10.x.1951, I. F. B. Common, 1 ♂ (C.S.I.R.O.). Merredin, 26.ix.1938, 1 ♀ (C.S.I.R.O.). Mogumber, 11-14.x.1938, 1 ♂, 1 ♀ (C.S.I.R.O.). Mullewa, Sept., L.J.N., 1 ♀ (W.A. Dep. Agric.). Perth, L. J. Newman, 1 ♀ (W.A. Dep. Agric.); 22.xi.1938, 1 ♀ (C.S.I.R.O.); Aug. 1948, 1 ♂, 2 ♀♀ (W.A. Dep. Agric.); 20-25.ix.1951, I. F. B. Common, 11 ♂♂, 9 ♀♀ (C.S.I.R.O.). Stirling Range, 7.x.1951, I. F. B. Common, 1 ♂, 1 ♀ (C.S.I.R.O.). Waroona, 9.xi.1948, A.B., 1 ♂, 2 ♀♀ (Nat. Mus.). Warren River, W. D. Dodd, 1 ♂, 2 ♀♀ (S. Aust. Mus.). Yanchep, 11-12.ix.1938, 3 ♀♀ (Qld. Mus.); 10-16.ix.1938, 3 ♂♂, 3 ♀♀ (C.S.I.R.O.).

Comments

P. dyscrita is a duller species than *P. ewingii* with the fore wings of a more uniform dull grey colour. The pale basal area of the hind wings usually

AUSTRALIAN ARMYWORMS, GENUS *PERSECTANIA*



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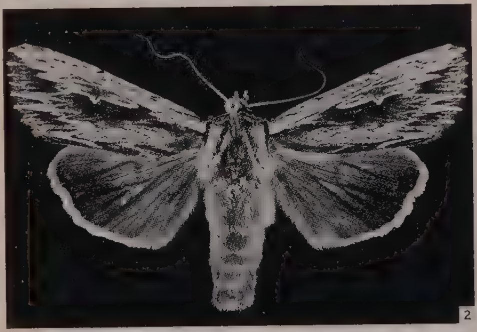

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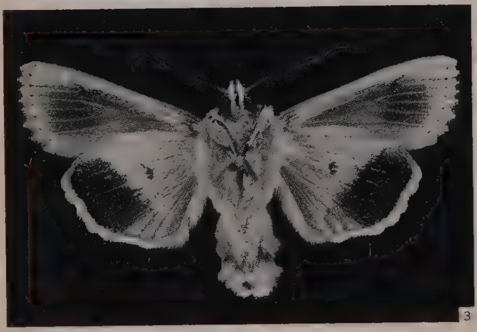

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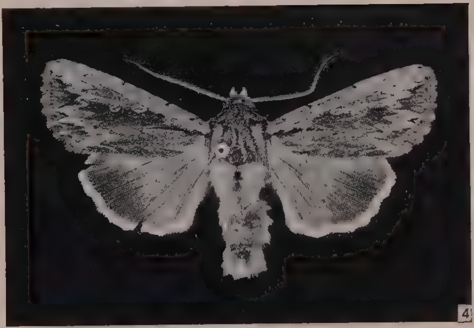

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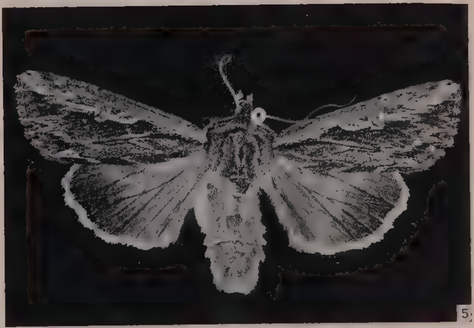

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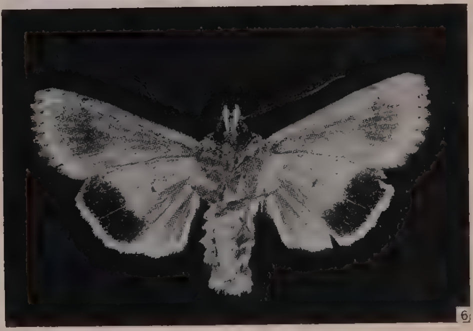

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serves to distinguish it, but the postmedial line of the fore wings (Fig. 4*B*), in which the dentations are less acute than in *P. ewingii* (Fig. 4*A*), is a more reliable character. The orbicular and reniform of the fore wing are more often separate in *P. dyscrita,* whereas in *P. ewingii* they are nearly always confluent. The under side of *P. dyscrita* is much whiter and the terminal fascia is therefore more distinct than in *P. ewingii.* Both sexes also lack the purplish tinge to the under side which is practically always present in males, and sometimes also to some extent in females, of *P. ewingii.*

Generally *P. dyscrita* is smaller than *P. ewingii* in both sexes, but it should be remembered that the size of both species varies considerably and may be dependent on the quantity of food available to the larvae. Adults reared from larvae taken from dense swarms, in which competition for food is severe, are usually less than average size. Also adults reared in the laboratory under certain unfavourable conditions may be small.

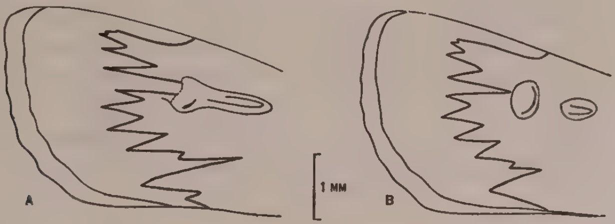

Fig. 4.—Distal half of fore wing of (*A*) *Persectania ewingii* (Westw.), and (*B*) *P. dyscrita*, sp. nov., showing postmedial line, orbicular, and reniform. (Camera lucida.)

If the determination of adults on the more superficial characters is at all doubtful, the genitalia provide excellent characters for separation. In the male, the curious shape of the clavus in *P. dyscrita* distinguishes it immediately from *P. ewingii.* The juxta is broader at the base with concave sides, whereas in *P. ewingii* the sides of the juxta are nearly parallel. In the female, the bursa copulatrix of *P. dyscrita* is relatively shorter than in *P. ewingii* and is of about uniform diameter when dilated. The ductus seminalis leaves the bursa copulatrix at its posterior end, whereas in *P. ewingii* it leaves the bursa copulatrix at its anterior end.

The fore wings of specimens of *P. dyscrita* from Western Australia have a slight ochreous suffusion and the markings are more distinct than in the type series and other specimens from eastern Australia. This may prove to be of subspecific significance.

Little is known of the ecology of *P. dyscrita.* It has a distribution in southern Australia, except Tasmania, rather similar to *P. ewingii* but appears to occur more commonly in inland areas where the summer rainfall is low. A series of specimens in the New South Wales Department of Agriculture were reared from larvae at Jerilderie, in the Riverina, where it apparently causes outbreaks at times. The outbreaks in the wheat belt of Western Australia described by Newman (1927) were probably also due to this species. There it was reported to have an annual life cycle, the larvae being present during the winter and the resulting adults not emerging until the following autumn. However, there are many records of adults of this species from Western Australia in the spring. In eastern Australia adults have been taken at Canberra from late September until early December and from February to April. This may indicate that two generations normally occur in both eastern and Western Australia. Intensive studies of the ecology of this species are needed to demonstrate clearly the differences between it and *P. ewingii.*

ACKNOWLEDGMENTS

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EXPLANATION OF PLATE 1

Fig. 1.—Upper side of male of *Persectania ewingii* (Westw.), Black Mountain, A.C.T., 3.xi.1952, I. F. B. Common (light trap) (C.S.I.R.O.).

Fig. 2.—Upper side of female of *P. ewingii* (Westw.), Black Mountain, A.C.T., 4.xii.1952, I. F. B. Common (light trap) (C.S.I.R.O.).

Fig. 3.—Under side of male illustrated in Figure 1.

Fig. 4.—Upper side of holotype of *P. dyscrita*, sp. nov., Black Mountain, A.C.T., 31.x.1952, I. F. B. Common (light trap) (C.S.I.R.O.).

Fig. 5.—Upper side of allotype of *P. dyscrita*, sp. nov., Black Mountain, A.C.T., 3.xi.1952, I. F. B. Common (light trap) (C.S.I.R.O.).

Fig. 6.—Under side of holotype of *P. dyscrita*, sp. nov.

THE AUSTRALIAN SYRPHID FLIES OF THE SUBFAMILY CERIOIDINAE (DIPTERA : SYRPHIDAE): SYSTEMATICS AND WING FOLDING

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Contents

Summary 100
Introduction 100
Systematics 101
Key to Australian species of the genus *Cerioides* 103
Description of species 104
The folding wings of *Cerioides breviscapa* (Saunders) and related species 125
Acknowledgments 128
References 129
List of species 130

Summary

The Australian representatives of this subfamily are recorded and nine new species described: *Cerioides ablepta, C. euchroma, C. lypra, C. optata, C. phya, C. picta, C. procapra, C. sphenotoma,* and *C. tolmera.* An account of the longitudinal wing folding, which occurs in a limited number of the species, is given.

Introduction

This paper deals briefly with the history of the systematics of the Australian Cerioidinae and includes descriptions of most indigenous species. It has been found that generic subdivision of the group based on the characters used by earlier workers is not practicable. For this reason, all the known species are at present referred to the genus *Cerioides.* The terminalia of the various species may provide good generic characters, but no definite conclusions can be reached until a critical study of the terminalia of a number of exotic species is undertaken. A generic revision, therefore, must await the examination of such material when it becomes available.

Until the appearance of Ferguson's paper (1926) dealing with this subfamily, only four valid Australian species were known. He more adequately described two of these species and added nine more. Two of the latter are homonyms, the same specific names having been used for quite different South American species. Shannon (1927) and Hardy (1945*b*) each described single species, making a total of 13 species. In addition there are several synonyms.

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Curran's and Hardy's species are reported to have longitudinally folding wings and now five of the 24 species included in this paper are known to possess this character.

SYSTEMATICS

Shannon (1925, 1927) subdivided the genus *Cerioides* into 5 distinct genera, basing his subdivision on the structure of the antennifer and on the shape of the abdomen. The antennifer shows a gradual increase in relative length from one species to the next and is therefore quite unsuitable for generic division. In *breviscapa* Saunders the antennifer is extremely short in both sexes, being only about as long as broad. In the male of *alaplicata* Hardy it is similar to that of *breviscapa,* while in the female it is considerably longer, varying from about ½ the length of the 1st antennal segment to almost the full length. In *opuntiae* Ferguson it is about as long as the 1st antennal segment, though there is some slight sexual dimorphism, the structure being shorter in the male. In the vast majority of species it is considerably longer, in general about 1½ times as long as the 1st antennal segment. There is also a group of a few species, including *tolmera,* sp. nov., *ablepta,* sp. nov., and *atacta,* nom. nov., in which it is twice as long.

The shape of the abdomen is a good specific character. The basal 2 segments vary from almost as wide as the succeeding segments to very narrow and elongate. In *opuntiae,* the male shows practically no constriction, but in the female there is a slight narrowing. The 1st 2 segments in both sexes are considerably wider than long. The group including *ornata* (Saunders) shows a condition, in both sexes, similar to that of the female *opuntiae.* The species *optata,* sp. nov. has the 1st segment even more constricted, but the 2nd has remained about the same as in the *ornata* group. The 1st segment is wider than long. In *mastersi* Ferguson the 1st and 2nd segments are both constricted, but there is only a slight "waisting" at the joint between them. The 2nd segment is here almost as long as wide. The species *breviscapa* also has only a slight "waisting," but the 2nd segment is as long as wide. In *atacta* the "waist" is more pronounced and segment 2 is noticeably longer than wide. The 1st segment is almost as long as its greatest width and does not vary much in the succeeding species, the increase and variation being almost entirely restricted to the 2nd and to some extent the succeeding segments. The greatest width of the 2nd segment is equal to that of the 1st. In *alaplicata* the condition in the female is similar to that in *atacta,* but in the male the 2nd segment is noticeably longer and its greatest width is less than that of the 1st segment. This condition of the male occurs in both sexes of *euchroma,* sp. nov. but is less pronounced, the 2nd segment being less than twice as long as broad. In *tolmera* and *ablepta,* like the male of *alaplicata,* this 2nd segment is more than twice as long as broad. In *subarmata* Curran, not only is this so, but the 3rd segment is reduced in width (and in size), so that the greatest width of the abdomen occurs at segment 4. In *procapna,* sp. nov. the 3rd segment is similar in shape to that of *subarmata,* but the 2nd segment is not quite twice as long as broad. In all other

Australian species examined, the greatest width of the abdomen is reached by the 3rd segment, though in many cases, particularly in the male, the 4th segment may be just as wide.

Using a combination of antennifer and abdomen, it is impossible to separate the Australian species into well-defined groups. The only species with the combination of short antennifer and constricted abdomen is *breviscapa*. There is a large group with long antennifer and constricted abdomen, but it cannot be separated sharply from *breviscapa* because of the sexual dimorphism of the antennifer in *alaplicata,* nor from the group with unconstricted abdomen because the 2 species *optata* and *mastersi* are intermediate in structure. The species *opuntiae,* though having a slightly shorter antennifer, could remain in the 2nd (large) group with long antennifer and unconstricted abdomen.

If the Australian species are to be divided into distinct genera it will have to be on characters other than those provided by the antennifer and the shape of the abdomen. Shannon has used the presence or absence of a plumula for subdivision within the genus but this structure, when it occurs in the Australian Cerioidinae, is not typical. It is best considered as a specific character, since it separates otherwise closely related forms and moreover in some species it is only weakly developed.

There is a single Australian species with a completely sclerotized metasternum but it differs from the genus *Polybiomyia* Shannon in that the antennifer is long, being distinctly longer than the 1st antennal segment. A number of species show the sternum approaching complete sclerotization.

An examination of the genitalia of the Australian species of *Cerioides* suggests that a satisfactory generic separation could be based on genitalia characters. To a large extent this separation would probably follow a division based on the shape of the abdomen. Species with unconstricted abdomen, together with *optata, mastersi,* and *tolmera,* form one group, while the rest of the species, with constricted abdomen, except *subarmata* and possibly *procapna,* form the other large group. The species *ablepta,* with completely sclerotized metasternum, is known only from the female so, for the present, it is considered on its own. Until an examination of the genitalia of exotic species is undertaken, a generic division of the Australian species seems unjustified. In this paper, therefore, they have been treated as species groups within the single genus *Cerioides.*

Ornata group, generally with unconstricted abdomen and long antennifer (the only exceptions being *optata, mastersi,* and *tolmera*): *ornata* (Saunders), *ornata australis* (Macquart), *apicalis* Ferguson, *lypra,* sp. nov., *euphara,* nom. nov., *alboseta* Ferguson, *mastersi* Ferguson, *tolmera,* sp. nov., *opuntiae* Ferguson, and *picta,* sp. nov. Probably also *sphenotoma,* sp. nov., *optata,* sp. nov., *saundersi* (Shannon), *mellivora* (Shannon), and *platypus* Ferguson, of which male specimens were not examined.

Subarmata group, with constricted abdomen, long antennifer, and folded wings, includes definitely only *subarmata* Curran. Probably also *procapna,* sp. nov., of which only a female specimen was examined.

Macleayi group, with constricted abdomen and long or short antennifer—long in all species except *breviscapa, phya,* and *alaplicata*—includes the following species: *macleayi* Ferguson, *euchroma,* sp. nov., *alaplicata* Hardy, *atacta,* nom. nov., *phya,* sp. nov., and *breviscapa* (Saunders). Probably also *doddi* Ferguson, of which only a female was examined.

Key to Australian Species of the Genus Cerioides

1. Abdomen not constricted at base 2
Abdomen definitely constricted at base 11

2 (1). Distinct plumula present 3
Plumula indistinct or absent 4

3 (2). Third abdominal tergite entirely black, 2nd tergite black with the hind margin yellow .... *C. mellivora* (Shannon)
Second, 3rd, and 4th tergites blackish with yellow posterior margins, 1st tergite reddish yellow, yellow laterally .... *C. saundersi* (Shannon)
First tergite black except for yellowish lateral borders, 2nd reddish brown with bright yellow apical border, 3rd and 4th segments dark with yellowish posterior borders .... *C. ornata* (Saunders)

4 (2). Pigmentation of the wing not extending into the "dip" of "R_{4+5}" 5
Pigmentation of the wing extending into the "dip" of "R_{4+5}" 7

5 (4). First abdominal segment entirely black; no median spot anterior to the scutellum .. *C. opuntiae* Ferguson
First abdominal segment with the latero-basal areas yellowish; median yellowish spot anterior to scutellum 6

6 (5). Third abdominal segment almost completely red, no coloured areas lateral to the large median one on scutum; setae of venter short (normal) .. *C. picta,* sp. nov.
Third abdominal segment with posterior ½ yellow, yellowish areas lateral to the small median one on scutum, extending to the transverse suture; setae of venter very long .... *C. lypra,* sp. nov.

7 (4). First abdominal segment completely black 8
First abdominal segment not completely black 9

8 (7). Third abdominal segment reddish brown except for black basal triangle, 2nd segment completely black (♀) or with narrow reddish border (♂) .... *C. apicalis* Ferguson
Third abdominal segment with only the posterior border red, 2nd with a wide reddish band (♂, ♀) .... *C. platypus* Ferguson

9 (7). Style white; 3rd abdominal segment with median protuberance .... *C. alboseta* Ferguson
Style dark; no protuberance on 3rd abdominal segment 10

10 (9). Third abdominal segment red except for black basal triangle, 2nd segment completely black with faint evidence of reddish apex (♀) .... *C. sphenotoma,* sp. nov.
Third abdominal segment with only apical margin red, 2nd segment completely black (♂) or with only apical band of red (♀) ...... *C. euphara,* nom. nov.

11 (1). Second abdominal segment distinctly not as long as its greatest width, style dark .... *C. optata,* sp. nov.
Second abdominal segment as long as its greatest width, style white (see also *breviscapa* and ♀ *alaplicata*) .... *C. mastersi* Ferguson
Second abdominal segment generally considerably longer than wide (only slightly so in *breviscapa, phya, doddi,* and ♀ *alaplicata*) 12

12 (11). Antennifer short, generally much shorter than 1st antennal segment (but approaching it in ♀ *alaplicata*) 13
Antennifer long, distinctly longer than the 1st antennal segment 14

13 (12). Median vertical facial marking, sexual dimorphism in antennifer and shape of abdomen . . . . *alaplicata* Hardy

Cruciform dark facial marking; sexes similar, vertex with 2 reddish spots . . . . *C. breviscapa* (Saunders)

Cruciform dark facial marking; vertex all reddish . . . . *C. phya*, sp. nov.

14 (12). Wing membrane more or less completely dusky, wings folded longitudinally, 3rd abdominal segment reduced in size 15

Wing membrane with definite darkened anterior border, 3rd abdominal segment of normal large size 16

15 (14). Second abdominal segment reddish brown with black apex and median dorsal band, 3rd segment with yellowish apex . . . . *C. subarmata* Curran

Second abdominal segment light reddish brown with yellowish apex, 3rd segment without distinct yellowish apex . . . . *C. procapna*, sp. nov.

16 (14). Pigmentation of the wing extending into the "dip" of "R_{4+5}" 17

Pigmentation of the wing not extending into the "dip" of "R_{4+5}" 19

17 (16). Yellowish median spot anterior to the scutellum 18

No median spot on mesonotum (2nd abdominal segment very long, red on contracted portion, otherwise black except for yellowish apical band; metasternum sclerotized below, across the meson) . . . . *ablepta*, sp. nov.

18 (17). Pigmentation of wing bordered posteriorly by *CuA* in basal ½ of wing; 1st abdominal segment black at base except laterally . . . . *tolmera*, sp. nov.

Pigmentation extending only to vena spuria; a pair of yellowish areas laterad to median spot on scutum; 1st abdominal segment yellow at base (and laterally) . . *atacta*, nom. nov.

19 (16). First and 2nd abdominal segments reddish, subcostal space pigmented . . . . *macleayi* Ferguson

First and 2nd abdominal segments dark, 1st with latero-basal areas yellow, 2nd with apex yellow; subcostal space clear . . . . *euchroma*, sp. nov.

First and 2nd abdominal segments black, with yellow band at apex of 2nd segment; subcostal space pigmented . . . . *doddi* Ferguson

Description of Species

Cerioides ornata (Saunders)

Plate 1, Fig. 1

Ceria ornata Saunders, 1845, Trans. Ent. Soc. Lond. **4**: 64.

Cerioides ornatus Ferguson, 1926*a* (partim), Proc. Linn. Soc. N.S.W. **51**: 142.

Ferguson has given a rather general description of this species. Both sexes are described here in full because the north Australian specimens differ from those obtained from the east coast of Queensland and New South Wales. The north Australian specimens are of the typical form while the Brisbane and other Queensland specimens are considered subspecifically distinct.

Male

Face yellowish with a vertical, dark median stripe, extended laterally in the region of the antennifer as a faint line towards the orbits. Lateral areas of the face dark reddish brown. Antennifer and surrounding area at the base reddish brown; antennae somewhat darker; style almost black. Vertex yellowish except around the ocelli where it is almost black. Antennifer almost twice as long as 1st antennal segment, which is slightly longer than the 2nd or 3rd segments.

Thorax blackish, finely granulose. Humeral angles and lateral ends of transverse suture yellowish. Dividing the anterior margin almost equally are 2 pollinose yellowish areas. Transverse suture also with yellowish pubescence somewhat aggregated at inner ends. Slight yellowish lateral patch just posterior to transverse suture; postero-lateral angles dark. Scutellum yellowish, slightly darker in the midline. Pleural segments yellowish. Postscutellum almost smooth. Legs light reddish brown, bases of the femora sometimes darkened. Hind trochanter with normal sparse hairs, a slight groove at apex. Hind tibia not produced apically into a spine. Middle femur with a brush of black setae basad and anterior, with long hairs along the posterior margin. Middle tibia with an apical row of about 9 teeth. Wings rather clear; anterior ½ darkly pigmented; the pigmentation bordered posteriorly by the vena spuria to the furcation of *Rs* and then by "R_{4+5}" to the wing margin and including the "dip" of the vein. Plumula present.

Abdomen only slightly constricted at base. Second segment slightly longer than the 1st; 3rd very much longer than the 2nd; 4th relatively small. First segment reddish black except for the yellowish lateral borders, more extensively pigmented at the base. Second with a bright yellowish apical border; basal portion reddish brown with a median almost black line accentuating the slight callosities of the lateral portions. Third black with yellowish posterior margin which may be darker reddish brown. Fourth similar, but with a bright gold pubescence. Venter rather similar in colouring to dorsal surface. Genitalia: aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges, somewhat reduced in size, elliptical in outline. Aedeagus only as long as claspers, very small and narrow.

Female

Similar to male except for the eyes, separated by an almost black band lying between the ocelli and the antennifer, and itself divided by a median reddish brown stripe.

Size

Length of body, excluding antennifer, ♂ 10-11 mm, ♀ 11.5-12 mm; length of wing, ♂ 8.5-9 mm, ♀ 10-10.5 mm.

Type: In the British Museum.
Type locality: NW. coast of Australia.
Distribution.—Most of north Australia.

The above description is based on specimens from Brocks Creek, N.T., which are considered to be of the typical form. Specimens in the Macleay Museum, Sydney, from Cape York and N. Coast, New Holland, are conspecific. I have also examined 3 specimens labelled Sydney. Specimens from the east coast of Queensland show distinctive features and are separated as a distinct subspecies considered to be *Ceria australis* Macquart 1850.

CERIOIDES ORNATA AUSTRALIS (Macquart)

Plate 1, Fig. 2

Ceria australis Macquart, 1850, Dipt. Exot. Suppl. **4**: 128.
Cerioides ornata Hardy, 1921, Aust. Zool. **2**: 13.
Tenthredomyia australis Shannon, 1925, Insec. Inscit. Menst. **13**: 54.
Tenthredomyia (*Pterygophoromyia*) *ornata* Shannon, 1927, J. Wash. Acad. Sci. **17**: 43.

Most authors have considered *australis* as a synonym of *ornata*. Though the 2 are closely allied and there is some confusion regarding the type locality of *australis*, as the type of *australis* is presumed lost, I prefer to consider *australis* as the form occurring in coastal Queensland and surrounding areas and so preserve the 2 names; *australis* then becomes a subspecies of *ornata*. As pointed out by Ferguson, it is preferable to consider that a mistake has been made regarding the length of the antennifer in *australis*, the antennifer being considerably longer than the 1st antennal segment.

Male

Similar to the typical form except that the yellow pigmentation of the pleural segments is confined almost entirely to the mesopleuron, with very little on the pteropleuron. The abdominal markings are also somewhat different. First segment with the lateral yellowish pigmentation much more restricted than in the typical form; 2nd with the callosities not quite so prominent. Further, the lateral yellowish spot on the thorax just posterior to the transverse suture of the typical form is quite reduced.

Female

Similar to the male except for the separated eyes.

Size

Length of body, excluding antennifer, ♂ 11 mm, ♀ 11-15 mm; length of wing, ♂ 9.5 mm, ♀ 10-12.5 mm.

Type: Presumed lost.

Type locality: Australia.

Distribution: Queensland and New South Wales.

I have not had the opportunity of examining the type of Macquart's species, but have examined specimens, which I consider to be conspecific, from Canberra, A.C.T., from Wanchep, N.S.W., and from Brisbane, Rockhampton, Ayr, Collinsville, Endeavour R., and Port Denison, Queensland. One specimen from Brisbane was reared from the wet comb of a beehive.

CERIOIDES SAUNDERSI (Shannon)

Tenthredomyia saundersi Shannon, 1925, Insec. Inscit. Menst. **13**: 53.
Tenthredomyia (*Pterygophoromyia*) *saundersi* Shannon, 1927, J. Wash. Acad. Sci. **17**: 43.

"*Male*. Plumula present. Ocellar triangle twice as long as its broadest width, yellow; frontal triangle yellow, a brownish stripe extending from antennal base to tubercle; a lateral brownish stripe on each side of lower face; humeri yellow; a bright yellow spot at outer ends of transverse suture and a yellowish pollinose spot at each of its inner ends; posterior half of scutellum yellow; mesopleura only with yellow spot; legs reddish-brown, four fore femora darkened basally, their tibiae darkened at the middle; first tergite reddish-yellow, yellow laterally; second, third and fourth tergites brownish-black with yellow post margins; hypopygium globose, brownish-black; wings dark brown on anterior half.

Length: 12.5 mm.; wings 10.5 mm.

Type: No. 27821, U.S. Nat. Mus.

Type Locality: N.S.W., Sydney. January 1900 (Mackay).

Distribution: Queensland. Burnett River (T. L. Bancroft); Mackay (G. Turner)."

The description of this species given by Shannon (1925, 1927) is repeated above because it is almost identical with that of *variabilis* Ferguson 1926 (non Kertesz 1903) from which it differs chiefly in the presence of the plumula and of a yellow posterior border to the 2nd abdominal segment of the male, in the latter character resembling *alboseta* Ferguson.

CERIOIDES MELLIVORA (Shannon)

Tenthredomyia (*Pterygophoromyia*) *mellivora* Shannon, 1927, J. Wash. Acad. Sci. **17**: 43.

"Closely related to *ornata* Saunders. Plumula present. Differs chiefly in having the yellow of the pleurae confined to the mesopleura and in having the second tergite black with the hind margin yellow and the third tergite entirely black. In *ornata*, the second tergite is almost entirely yellow and the hind margin of the third is yellow. The ocellar triangle of the male is equilateral and the callosities on the second tergite are more prominent than in *ornata*. In the ♀ the eyes converge as closely together at the vertex as in the ♂ but widen rapidly downwards; the centre of the frons has a very large black spot which includes the ocelli. The fifth tergite is obscurely reddish-yellow. Length, about 12 mm., not including antennifer which is 1.5 mm.; antennifer and antennae combined, 5 mm.; wing 13 mm.

Described from 2 males and 4 females; 8 additional specimens are in the British Museum.

Type: Holotype ♂, allotype ♀, in the British Museum; paratypes in the U.S. National Museum. Cat. No. 40105 U.S.N.M.

Two specimens have been reared and the puparia are mounted with the specimens and bear the label 'Larvae live on honey in native bee's nest.' (Note by donor.)

Type Locality: Burpengary, South Queensland (T. L. Bancroft)."

I have not examined specimens of this species but have given Shannon's description to enable recognition of the species.

CERIOIDES EUPHARA, nom nov.

Plate 1, Fig. 3

Cerioides variabilis Ferguson, 1926*a*, Proc. Linn. Soc. N.S.W. **51**: 146—non Kertesz 1903.

As Kertesz (1903) described a distinct species, *variabilis*, from Bolivia, Ferguson's specific name is invalidated. Ferguson described both sexes of this species and also indicated the range of variation which is known to occur. These additional characters are added: Postscutellum with numerous faint rugae. Hind trochanter with a tuft of short, stout, black bristles (only in ♂). Hind tibia not produced into a spine. Middle femur with a brush of short black setae at base. Middle tibia with an apical row of about 12 spines. Genitalia of male: aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges, in lateral view, slightly longer than broad at base, large, surface irregularly, slightly grooved. Aedeagus stout, considerably longer than claspers, truncate.

Size

Length of body, excluding antennifer, ♂ 10-11 mm, ♀ 9-10.5 mm; length of wing, ♂ 8.5-9.5 mm, ♀ 8.5-9.5 mm.

Types: In the Australian Museum, Sydney.
Type locality: Queensland. Westwood.

QUEENSLAND: Westwood; Eidsvold; Gayndah; Rockhampton; Port Curtis; Chinchilla; and Dulacca.

The species is very similar to *saundersi* but lacks a plumula. It also shows superficial similarity to *ornata*, but can be distinguished on the abdominal markings. Ferguson (1926*b*, p. 517) states that *variabilis* is probably synonymous with *saundersi*, but it was not until 1927 that Shannon separated *saundersi* as the type species of his subgenus *Pterygophoromyia*, typified by the presence of a plumula.

CERIOIDES ALBOSETA Ferguson

Plate 1, Fig. 4

Cerioides alboseta Ferguson, 1926*a*, Proc. Linn. Soc. N.S.W. **51**: 145.

Both sexes were described by Ferguson. These additional characters are added: Postscutellum with only very faint rugae on posterior ½. Hind trochanter with very short hairs, strong groove at apex. Hind tibia not produced into a spine. Middle femur with a brush of short, black setae at base. Middle tibia with an apical row of about 9 spines. Genitalia of male: aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges, in lateral view, as long as broad at base, large, surface irregularly slightly grooved. Aedeagus stout, somewhat shorter than claspers, truncate.

Size

Length of body, excluding antennifer, ♂ 11.5 mm, ♀ 11-12 mm; length of wing, ♂ 9.5 mm, ♀ 11 mm.

Types: In the Australian Museum, Sydney.
Type locality: Queensland. Gordonvale (Dec. 1919).

QUEENSLAND: Gordonvale; Cairns district; Port Curtis; Somerset, Brisbane; Kuranda (Dec. 1927, A. P. Dodd); Mackay (1900, W. W. Froggatt).

The species is similar to *euphara,* but can be separated by the white style and the median protuberances on the 3rd and 4th abdominal segments.

CERIOIDES PLATYPUS Ferguson

Cerioides platypus Ferguson, 1926*a,* Proc. Linn. Soc. N.S.W. **51**: 144.

Both sexes were described by Ferguson.

Types: In the Australian Museum, Sydney.

Type locality: South Australia.

Distribution.—In addition to the type locality Ferguson also records the species from Magnetic I., Queensland.

This species is considered to be allied to *euphara,* from which it differs as follows: The 1st abdominal segment is entirely black and the 2nd has a broad apical reddish orange band in both sexes. The posterior femora of the male have a flange-like thickening and the tarsi are greatly flattened.

CERIOIDES APICALIS Ferguson

Plate 1, Fig. 5

Cerioides apicalis Ferguson, 1926*a,* Proc. Linn. Soc. N.S.W. **51**: 147.

The species was described from a single male specimen. I have examined a male and a female taken in copula as well as 2 other specimens.

Male

Agrees in all essentials with the description given by Ferguson, to which may be added the following characters: Hind trochanter with normal sparse hairs. Hind tibia not produced apically into a spine. Middle femur with a posterior fringe of long hairs. Lateral hind margin of the 4th tergite produced into a short spine. Genitalia: aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges, reduced, elongate ellipsoid with slight lateral flange. Aedeagus not visible beyond the claspers.

Female (allotype)

Head much blacker than in male, small yellowish spot external to the antennifer absent and patch on each side of face very reduced. Except for these 2 patches the head is completely black. Antennifer dark reddish brown. Antennae black at base, but dark reddish brown at apex. Style black. Thorax as in male. Abdomen similar to the male, but with the 2nd segment completely black. Third segment very large, almost concealing the 4th, which shows a slight median protuberance as well as the lateral spines. Wings and legs as in male.

Size

Length of body, excluding antennifer, ♂ 12 mm, ♀ 13 mm; length of wing, ♂ 10 mm, ♀ 11.5 mm.

Types: Holotype ♂ in Australian Museum, Sydney. Allotype ♀ in Division of Entomology Museum, C.S.I.R.O., Canberra. The allotype was mounted with the male specimen taken in copula with it, but has been remounted and the 2 specimens separated.

Type locality: Holotype, Gayndah, Queensland; allotype, Goondiwindi, Queensland.

QUEENSLAND: Gayndah; Goondiwindi (K. H. L. Key, 7.xi.1936), 1 ♂, 1 ♀, Goondiwindi (F. H. Roberts, Nov. 1927), 1 ♂; Dulacca (2.xii.1939, J. E. Tesch).

This is a very distinct species characterized by the almost black head and thorax and by the pigmentation of the wing, the pigment extending back to *CuA* from the base to as far as *m-cu*, then bounded by the vena spuria to *r-m* and "R_{4+5}" to the wing margin. The subcostal space is clear.

CERIOIDES SPHENOTOMA, sp. nov.

Plate 1, Fig. 6

Female (*holotype*)

Face with a reddish brown median stripe completely surrounding the base of the antennifer but not extending laterad towards the orbit. Lateral margins of face extending from the oral margins to the eyes, black-brown. Antennifer reddish brown, darker towards the apex. First and 2nd antennal segments dark reddish brown, 3rd lighter, style dark. Eyes well separated, closest in the ocellar region. Vertex reddish, slightly darker round the ocelli. Between the ocelli and the base of the antennifer a pair of darkened patches extending from the eye margin almost to the midline. Antennifer considerably longer than the 1st antennal segment, which itself is a little longer than the 2nd but not quite as long as the 3rd segment.

Thorax dark reddish brown to black, finely granulose. Humeral angles and a patch on lateral margin at transverse suture reddish yellow. Yellowish pubescence at the inner end of the transverse sutures. Scutellum dark reddish, black basally in the median area. Pleural segments dark. Postscutellum with numerous fine rugae. Legs reddish, slightly darkened at the bases of the femora. Wings slightly clouded, with dark brown anterior margin, the dark coloration bounded posteriorly by the vena spuria almost to the *r-m* cross vein and then just below "R_{4+5}" to the wing margin, filling the slight "dip" in this vein. Subcostal space coloured.

Abdomen only slightly contracted at base. First 2 segments of about equal size, 3rd large, 4th smaller. First segment reddish, with the median area, particularly at the posterior margin, darker; 2nd dark, almost black, with indications of a transverse, median, crescentic reddish line; 3rd reddish except for a blackish triangle covering the base and with its apex at the middle of the segment; 4th reddish with a distinct yellow pubescence. Venter rather dark except for the apical margins.

Size

Length of body, excluding antennifer, ♀ 10 mm; length of wing, ♀ 9.5 mm.

Type: Holotype ♀ in Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Chinchilla, Queensland (Oct. 1927, A. P. Dodd).

The species is described from a single female, which shows a superficial resemblance to *apicalis* Ferguson, particularly in the coloration of the 3rd and 4th abdominal segments. It differs in the pigmentation of the wings, of the 1st and 2nd abdominal segments, and of the head.

CERIOIDES LYPRA, sp. nov.

Plate 1, Fig. 7

Male (holotype)

Face almost completely white except for slight darkening of the midline and on the lateral cheeks. Antennifer light reddish brown. Basal 2 segments of antenna black, apical segment dark reddish brown. Style black. Vertex of same general colour as the face. Eyes touching for the middle 1/3 of the distance between the ocelli and base of antennifer. Antennifer distinctly longer than 1st antennal segment, which is slightly longer than the 2nd or 3rd segments. Style quite long.

Thorax blackish, finely granulose. Humeral angles and an area just anterior to the transverse suture yellowish. Transverse suture with yellowish pubescence aggregated at inner ends. Anterior margin of thorax also with 2 areas of yellowish pubescence. Extending from the transverse suture to inner side of postero-lateral border an irregular yellowish band, postero-lateral borders yellowish. Scutellum yellowish with a darker median area and lateral borders. Pleural segments yellowish, the pigmentation darkening ventrally. Postscutellum distinctly grooved. Legs very pale yellowish brown with the bases of the femora slightly darker. Hind trochanter with very long hairs. Hind tibia with the mesal apical angle slightly more produced than the lateral one, but without a definite spine. Hind femur rather swollen. Middle femur with 2 strong carinae ventrally and an area of short bristles anteriorly on the basal 1/3 of femur. Middle tibia with an apical row of about 6 spines. Wings light smoky, anterior ½ darker, the pigment bordered posteriorly by the vena spuria to the furcation of *Rs* and thence by "R_{4+5}" to the wing margin, but not including the "dip" of this vein. Subcostal space clear.

Abdomen only slightly contracted at base. First 2 segments of about equal size, 3rd segment slightly longer, 4th segment quite large. First segment black with the base and lateral margins yellowish; 2nd segment completely black; 3rd and 4th segments black, but with wide apical yellowish bands. Venter black except for the apical margins, clothed in very long white hairs, in this respect being quite distinct from other Australian species. Genitalia: aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges, in lateral view as long as broad at base, large, with a definite elongated carina, mesal margin towards apex excised. In ventral view the claspers are considerably longer than broad. Aedeagus stout, considerably longer than claspers, truncate.

Size

Length of body, excluding antennifer, ♂ 10.5 mm; length of wing, ♂ 8 mm.

Type: Holotype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Bathurst I., N.T. (T. G. Campbell, 5.x.1933).

The specimen under examination appears to be freshly emerged and so shows less pigmentation than would be expected. This is borne out by the appearance of the wing membrane and the wrinkling of the surface of the body to a slight extent. Superficially the species resembles specimens from Aru Is. which are tentatively placed in *relicta* Walker, but it is quite distinct from other known Australian forms.

CERIOIDES OPUNTIAE Ferguson

Plate 1, Fig. 8

Cerioides opuntiae Ferguson, 1926*a*, Proc. Linn. Soc. N.S.W. **51**: 143.

Ferguson has described only the male of this species though specimens of both sexes from Cuttebrai Creek, with the same data as the type, are present in the Division of Entomology Museum, C.S.I.R.O., Canberra. The distinctive features of the female are given below.

Male

Additional characters include: Hind trochanter with fairly long hairs. Hind tibia not produced apically into a spine. Middle femur with a posterior fringe of long hair, basal spines reduced. Middle tibia with an apical row of 5 or 6 spines. Genitalia: Aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges, reduced, in lateral view not as long as broad at base, triangular. Aedeagus slightly but definitely longer than claspers.

Female

Similar to the male. Eyes widely separated, the area between the ocelli and almost to the base of the antennifer black; slightly sunken in the middle. Abdominal markings slightly different. Second abdominal segment with the lateral basal angles distinctly reddish brown (very dark, almost black, in some specimens). These lateral, triangular pigment areas extend about 2/3 of the distance towards the centre of the basal margin and almost to the posterior margin of the segment laterally.

Size

Length of body, excluding antennifer, ♂ 8.5-9 mm, ♀ 9.5-10 mm; length of wing, ♂ 6.5-7 mm, ♀ 8.5-9 mm.

Types: Holotype ♂ in the Macleay Museum, Sydney; allotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Cuttebrai Creek, N.S.W.

NEW SOUTH WALES: Cuttebrai Creek; Biniguy; 10 miles NW. Nyngan; 20 miles S. Milparinka; Nevertire. QUEENSLAND: Dalby; Taroom; Gravesend; Chinchilla; Kalapa; Goondiwindi. NORTHERN TERRITORY: 5 miles N. Noccatunga; Brocks Creek.

This is a very distinct species with very little pigmentation in the wings and with the antennifer abnormally short, only about as long as the 1st antennal segment. This structure is slightly shorter in the male than in the female. The species has been bred from decaying prickly pear and has also been collected at flowers of wilga and of *Hakea*.

CERIOIDES PICTA, sp. nov.

Plate 1, Fig. 9

Male (holotype)

Face with a narrow dark median stripe expanding in the region of the antennifer to reach the orbit. Lateral margins of face extending from the oral margins to the eyes, black. Antennifer and antennae almost black, scape black. Eyes touching for about ½ the distance between the ocelli and the base of the antennifer. Vertex red, dark around the ocelli. Antennifer considerably longer than the 1st antennal segment, which itself is a little longer than the 2nd but not quite as long as the 3rd segment.

Thorax black, finely granulose. Humeral angles yellowish, lateral margin back to the transverse suture, a small area just posterior to transverse suture, scutellum, and a large rounded median patch just anterior to the scutellum reddish. Most of mesopleuron and small areas of the pteropleuron and sternopleuron reddish yellow. Postscutellum mostly smooth in the median area. Legs light reddish, except for the black coxae and trochanters and darkened tarsal segments. Hind trochanter with normal short hairs. Hind tibia not produced apically into a spine. Middle femur with a strong, though blunt, black, ventral tooth near the base. Middle tibia with an apical row of about 9 spines. Wings clear in the hind ½, with sparse irregular pigmentation in the anterior ½, bordered posteriorly by the vena spuria in the basal ½, and then by "R_{4+5}" to the wing margin but not including the "dip" of the vein. Subcostal space clouded.

Abdomen very slightly, if at all, constricted at base. First three segments of about equal size, 4th much larger. The 3rd is considerably shorter than normal. First segment reddish at base and at lateral margins, thus leaving a black, apical triangular area extending over the full apical margin; 2nd completely black; 3rd completely reddish except for a small median black basal zone; 4th black, with a wide reddish apical band. Venter dark, except for the apices of the segments. Genitalia: aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges, somewhat reduced, almost as long as broad at base, more or less triangular, posterior margin excised. Aedeagus stout, slightly but definitely longer than claspers.

Size

Length of body, excluding antennifer, ♂ 9 mm; length of wing, ♂ 8 mm.

Type: Holotype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: "G'bluie, 2.11.1926" (Gundabloui, northern N.S.W.).

The species is described from a single male which shows some superficial recemblance to *opuntiae* but differs in the shape and markings of the abdomen and in the presence of the large median reddish patch on the thorax.

Cerioides optata, sp. nov.

Plate 1, Fig. 10

Female (holotype)

Face rather dark, a wide median black stripe extending laterally just below the level of the antennifer to the orbit and again above the antennifer to the vertex. Lateral and lower portions of the face dark so that there remain only 2 pairs of yellowish areas, one lateral to the antennifer and the other somewhat below it. Antennifer reddish brown, slightly darker at apex. First and 2nd antennal segments dark reddish brown, 3rd and scape slightly lighter in colour. Vertex dark reddish brown, black around the ocelli. Antennifer considerably longer than the 1st antennal segment, which itself is longer than the 2nd and about as long as the 3rd segment.

Thorax dark reddish brown to almost black. Humeral angles and a patch on lateral margin just anterior to the transverse suture reddish. Little yellowish pubescence at the inner end of the transverse sutures. Pleural segments dark. Postscutellum with very fine rugae. Legs reddish, darkened at the basal ½ of the femora, middle of the tibiae, and at the tarsi. Wings slightly clouded, somewhat darker along the anterior ½, the dark coloration more or less bounded by the vena spuria to the *r-m* cross vein and then by "R_{4+5}," including the slight "dip" of this vein, to the wing margin. Subcostal space clouded.

Abdomen noticeably contracted at the base though the 1st 2 segments are still broader than long. First segment slightly shorter than the 2nd, 3rd very large, 4th quite small. There is very little "waisting" at the joint between the 1st and 2nd segments. The 3rd is very wide, occupying the greatest width of the abdomen. First segment reddish brown, darker laterally; 2nd with the apical ½ reddish yellow, basal ½ darker, particularly in the median area; 3rd black with a wide reddish yellow apical margin; 4th similar but covered with a yellow pubescence. Venter rather dark except for the apices of the segments.

Size

Length of body, excluding antennifer, ♀ 11 mm; length of wing, ♀ 11 mm.

Type: Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Australia (Bancroft coll.).

The species, which is notable for the shape of the abdomen, is described from the single female type. In addition to the shape of the abdomen, the body markings are distinctive.

CERIOIDES MASTERSI Ferguson

Plate 1, Fig. 11

Cerioides mastersi Ferguson, 1926a, Proc. Linn. Soc. N.S.W. **51**: 151.

Ferguson described this species from a single female bearing the collection label, South Australia. I have 2 male specimens from Brisbane which I consider to be of this species, but have refrained from erecting an allotype for one of them. It remains to be ascertained by further collecting whether this is a widespread species or whether some mistake has been made in the labelling of the specimens.

Male

Face with a reddish brown median stripe, extending as a wide band just below the antennifer to the orbit and continuing around the base of the antennifer. Extreme lateral margins of the face dark; a dark line lying between this marginal one and the median stripe dividing the yellow area almost equally. Antennifer and antennae light reddish brown. Style light, white at apex. Eyes touching for only a short distance. Vertex yellowish, somewhat darker laterally and almost black around ocelli. Antennifer considerably longer than the 1st antennal segment, which itself is not quite as long as the 2nd, but is about equal to the 3rd segment. Style rather long, about ½ the length of the 3rd antennal segment.

Thorax dark reddish brown to black, finely granulose. Humeral angles and a patch on lateral margin at transverse suture yellowish. Yellowish pubescence at inner ends of the transverse suture. Scutellum yellowish except for the lateral margins and a median area which are darker. Mesopleuron with a vertical yellowish patch. Legs reddish brown, lighter at the bases and apices of the segments. Hind trochanter with normal sparse hairs. Hind tibia not produced apically into a spine. Middle femur with a short strong carina near base and a basal group of short bristles. Middle tibia with an apical row of 5 or 6 spines. Wings slightly clouded, with dark brown anterior margin, the dark coloration bounded posteriorly by the vena spuria to the *r-m* cross vein and then by "R_{4+5}," and including the "dip" of that vein, to the wing margin. Subcostal space clouded.

Abdomen obviously contracted at the base, 1st segment not quite as long as broad, 2nd as long as its greatest width, 3rd and 4th segments quite large. Only slight "waisting" at the joint between the 1st and 2nd segments. First segment with the basal ½ dark reddish brown, apical ½ yellowish except for the dark apical border; 2nd yellowish on the basal 1/3, the remainder dark; 3rd and 4th dark reddish brown with narrow yellow apical borders. Genitalia: aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges; in lateral view as long as broad at base, small, triangular, surface more or less plane. Aedeagus stout, large, almost twice as long as claspers, rounded truncate at apex.

Size

Length of body, excluding antennifer, ♂ 8.5-10 mm; length of wing, ♂ 8-9 mm.

Type: Holotype ♀ in the Australian Museum, Sydney.

Type locality: South Australia.

Distribution.—South Australia and Queensland. New locality. Brisbane (Jan. 1902, T. Batchelor).

The 2 specimens from Brisbane were taken hovering round a nest of the paper-nest wasp, *Polistes* sp. In the shape of the abdomen this species shows some similarity to *optata* but differs in the body colouring.

CERIOIDES TOLMERA, sp. nov.

Plate 1, Fig. 12

Male (holotype)

Face yellow with a broad, median, very dark brown stripe occupying about ½ of its width and with a narrow band extending laterally just below the antennifer to the orbit. Lateral margins of face extending from the oral margins to the eyes, black-brown. Antennifer reddish brown, darker towards the apex. First and 2nd antennal segments dark reddish brown, 3rd lighter. Style slightly darker than 3rd segment. Eyes contiguous for only the middle 1/3 of the distance between ocelli and antennifer. Vertex mainly yellowish but brownish round ocelli. Antennifer twice as long as the 1st antennal segment, which itself is equal in length to the 2nd. Third segment shorter than the 2nd.

Thorax black, finely granulose. Humeral angles and a patch on lateral margin at transverse suture yellowish. Some yellowish pubescence on transverse suture. Scutellum and a large median spot anterior to scutellum yellowish. Lateral margins of the scutellum of a slightly darker colour. Pleural segments black. Postscutellum with an almost smooth, matte surface. Legs reddish brown, but with the basal halves of the femora darker. Hind trochanter with normal short hairs. Hind tibia with a short spine on the ventro-mesal aspect of the apex. Middle femur with the setae and hairs reduced. Middle tibia with an apical row of 5 or 6 spines. Wings very pale brown with dark brown anterior margin, the dark coloration bounded posteriorly by *CuA* as far as *m-cu* and then by the vena spuria as far as the *r-m* cross vein and extending into the "dip" of "R_{4+5}." The subcostal space is clear.

Abdomen strongly contracted at base. First segment short and narrowed from base to apex; 2nd very long and narrow, basal portion subcylindrical, apex widening slightly; remaining segments wide, the 3rd about equal in length to the 4th. First segment dark at base except for lateral margins, apex reddish brown; 2nd yellow on contracted portion except for a dark dorsal median stripe; expanded apical portion dark except for a yellowish apical band; 3rd black with a distinct yellowish apical band; 4th black but covered with a fine yellowish pubescence and with a thin reddish yellow apical band. Venter blackish, 1st segment with a yellow apical band. Genitalia reddish brown;

aedeagus normally hidden by the 4th abdominal sternite. Claspers obvious, not produced laterally into definite flanges; in lateral view twice as long as broad at base, 5-sided. Aedeagus thin and tapered, considerably longer than claspers, more or less pointed.

Female (allotype)

Similar to the male except for the widely separated eyes, and sexual characters of the legs. Vertex behind the ocelli yellowish with a a partial median dark stripe. The black frons diverges markedly from the ocelli towards the antennifer and is strongly corrugated over a large area, which is divided by a rather wide smooth median stripe. The 3rd abdominal segment somewhat larger than the 4th. In other characters the female is similar to the male.

Size

Length of body, excluding antennifer, ♂ 13.5 mm, ♀ 14 mm; length of wing, ♂ 10.5 mm, ♀ 11 mm.

Types: Holotype ♂, allotype ♀, and 4 paratype ♂♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: A.C.T. Cotter River, near Canberra (7.i.1931, L. F. Graham, and 31.xii.1945, E. F. Riek).

Superficially this species resembles *subarmata* Curran but, in addition to the marked difference in genitalia, it can be distinguished by the wing pigmentation, the median spot on the mesonotum, and the absence of wing folding. Excluding the *subarmata* group this is the only species with a definitely petiolate abdomen, in which the aedeagus is normally hidden by the 4th abdominal sternite.

CERIOIDES SUBARMATA Curran

Plate 2, Figs. 1, 2

Cerioides subarmata Curran, 1926, Proc. Linn. Soc. N.S.W. **51**: 133.

Cerioides subarmata Curran and Bryan, Ferguson, 1926*a*, Proc. Linn. Soc. N.S.W. **51**: 151; Hardy, 1945*a*, Ent. Mon. Mag. **81**: 93; Hardy, 1945*b*, Proc. Roy. Soc. Qd. **56**: 81.

Monoceromyia austeni Shannon, 1927, J. Wash. Acad. Sci. **17**: 45.

Previous authors have credited this species to Curran and Bryan, but as stated in the original publication (p. 129) the new species were described by Curran alone. Bryan, in correspondence with Ferguson, who saw the paper through the press, stated, "Perhaps you had better insert in the paper, 'Descriptions by C. Howard Curran' as I had nothing to do with that part of it."

This is a very distinctive species, with folding wings, the membrane of which is completely dusky, though somewhat darker in the anterior ½. It is noteworthy because of the separated eyes of the male. In the wing venation an appendix may be present on vein "R_{4+5}" (as described for *austeni*) or absent (as in the description of *subarmata*). Shannon (1927) apparently was not aware of Curran's earlier work when he described this species.

Only the male of the species has been described. The female is described below.

Male

In addition to the characters already recorded: Hind trochanter with sparse hair, but produced into a strong, blunt tooth on the ventral side. Hind tibia with a spine developed from a short sharp carina on the mesal surface near the apex, so that the spine lies towards the inner side. Hind femur rather strongly excavated behind, where it is bordered with long hairs. Middle femur with a brush of black setae basal and anterior and with long hairs along posterior margin. Middle tibia with an apical row of 5 or 6 spines. Genitalia: aedeagus normally hidden by the 4th abdominal sternite. Claspers very much reduced, produced laterally into definite semicircular flanges. Aedeagus quite definite, large, apex truncate.

Female (allotype)

Head similar to the male except that the eyes are more widely separated and the reddish brown areas more extensive. Thorax and abdomen very similar, 3rd abdominal segment small as in the male, 4th very large, 5th quite small. Legs lacking the sexual characters of the male, but with the hind trochanter produced ventrally into the large blunt tooth.

Size

Length of body, excluding antennifer, ♂ 11-11.5 mm, ♀ 13 mm; length of wing, ♂ 8 mm, ♀ 11 mm.

Types: Holotype ♂ in the Bishop Museum, Honolulu. Allotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Brisbane, Queensland.

QUEENSLAND: Brisbane; Sunnybank; Brisbane (9.ix.1945, E. F. Riek); Brisbane (9.x.1923, H. Hacker).

CERIOIDES PROCAPNA, sp. nov.

Plate 2, Fig. 6

Female (holotype)

Face yellowish with a median, dark, almost black, stripe extending laterally in the region of the antennifer to the orbits. Base of antennifer lighter in colour than the surrounding area of the stripe. Antennifer and antennae of an even reddish brown. Style a little darker than the antennae. On the lateral area of the face there is another, upwardly sloping, stripe, lighter in colour than the median stripe and divided longitudinally by a paler band. Eyes well separated and diverging slightly from the vertex, which is yellowish red, darkening to almost black laterally. Area between ocelli and base of antennifer black, sharply defined on the anterior margin, but grading in colour posteriorly. Antennifer somewhat longer than 1st antennal segment, but not twice as long. Second and 3rd segments of about equal size, slightly shorter than the 1st. Style short.

Thorax blackish, finely granulose. Humeral angles and an area extending back to behind the transverse suture reddish yellow. Scutellum evenly reddish brown. Mesopleuron with very narrow posterior margin slightly lighter in colour than the dark pleural segments. Legs reddish brown, with the femora showing a slight basal darkening. Wings smoky, folded longitudinally when at rest. Both the wings of the holotype show this folding but in the other specimen the set wings are flat, though the evidence of the fold is quite obvious. The anterior ½ of the wing is slightly darker than the posterior, more so in a specimen from Brisbane. There is very little "dip" in vein "R_{4+5}," but otherwise the venation is normal.

Abdomen strongly contracted at base. First segment short and narrowed from base to apex; 2nd moderately long, basal ½ subcylindrical, apex widening somewhat, but not as wide as base of 1st; remaining segments wide. However, the 3rd segment is relatively small as compared with other species, being only about ½ as long as the 4th, and not reaching the full width of the abdomen. The nearest approach to this condition is to be seen in both sexes of *subarmata.* First segment dark except for the reddish brown apex; 2nd reddish brown with a wide yellowish apical border; 3rd evenly dark; 4th with a wide reddish brown apical border. Venter dark except for the apical border of the 4th segment.

Size

Length of body, excluding antennifer, ♀ 8 mm; length of wing, ♀ 7 mm.

Type: Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Eidsvold, Queensland.

QUEENSLAND: Eidsvold (15.ix.1929); Brisbane (12.xi.1912, H. Hacker).

The species is known from 2 females which, on wing structure, are similar to *subarmata.* It differs in the coloration of the face and abdomen and the relative length of the abdominal segments.

CERIOIDES ABLEPTA, sp. nov.

Plate 1, Fig. 17

Female (holotype)

Face yellow with a broad, median bright reddish brown stripe enclosing a narrow, median, yellow stripe and extending to the antennifer and beyond to the vertex. Antennifer and antennae evenly reddish brown. Style missing. Eyes well separated and diverging slightly from the vertex, which is mainly reddish brown, but has yellowish lateral areas. Between ocelli and base of antennifer a broad transverse dark band separated by a distinct median reddish brown stripe. Antennifer twice as long as 1st antennal segment, which is similar in length to the 2nd and slightly longer than the 3rd segment.

Thorax blackish, finely granulose. Humeral angles and an area on lateral margin just anterior to transverse suture yellowish. Slight whitish pubescence on transverse suture. Postero-lateral margins yellowish. Scutellum reddish brown with the narrow anterior margin darker. Mesopleuron with the posterior margin yellowish. Metasternum sclerotized below so that the segment is completely girdled. Legs reddish brown but with the basal halves of the femora darker. Wings very pale brown with dark brown anterior margin, the dark coloration bounded posteriorly by the vena spuria almost to the *r-m* cross vein and then by "R_{4+5}" to the wing margin. "R_{4+5}" without the characteristic "dip," but with a distinct appendix directed posteriorly. Slight darkening along *CuA*. Wing apparently without longitudinal folding.

Abdomen strongly contracted at base. First segment short and narrowed from base to apex, 2nd very long and narrow, basal portion subcylindrical, apex widening only slightly; remaining segments wide, the 3rd about equal in length to the 4th. First segment dark except for the extreme baso-lateral margins and the apex, which are reddish brown; 2nd reddish brown on contracted portion, dark on expanded portion except for the reddish brown apex; 3rd and 4th dark, with yellowish pubescence and with reddish brown apices, these apical bands being somewhat raised above the general surface of the rest of the segment. Venter dark except on petiole and apices of the segments.

Size

Length of body, excluding antennifer, ♀ 9.5 mm; length of wing, ♀ 8.5 mm.

Type: Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: National Park, N.S.W.

The species is described from a single female, which can be distinguished from *subarmata* and *tolmera*, which it resembles in the structure of the abdomen, by the wing pigmentation and the coloration of the abdomen and of the pleural segments. The completely sclerotized metasternum separates it from all other Australian species.

CERIOIDES ATACTA, nom. nov.

Plate 1, Fig. 13

Cerioides fascialis Ferguson, 1926*a*, Proc. Linn. Soc. N.S.W. **51**: 150—non Kertesz 1903.

Kertesz (1903) described *Ceria fascialis* from Paraguay. This species is quite distinct from the Australian *Cerioides fascialis* Ferguson 1926. Ferguson's description was based on a single female taken at Kuranda. I have examined a series of 3 males and 5 females collected at Brocks Creek, N.T., which I consider to be of this species, though possibly of a distinct subspecies. Female specimens from Brocks Creek differ slightly from the type in that the mesopleuron, sternopleuron, and portion of the pteropleuron are bright yellow. The facial markings and scutellum are also slightly different.

The male of this species has not been described, so I give a description of the males from Brocks Creek.

Male

Similar to the female except that the 1st and 2nd abdominal segments are slightly more elongate. Further the eyes of the male meet for a short distance in the midline, obliterating the dark patch which occurs in the female on each side just posterior to the antennifer. Hind trochanter with long hairs, slightly produced ventrally. Hind tibia elongated mesally into a strong spine. Hind femur slightly swollen, with strong black bristles on the apical ½ of the ventral margin. Middle femur with the setae and hairs reduced. Middle tibia with an apical row of 5 or 6 spines. Genitalia: aedeagus not hidden by the 4th abdominal sternite, much longer than claspers, 4 times as long as broad at base, tapering to a rather sharp point. Claspers much reduced, almost absent.

Size

Length of body, excluding antennifer, ♂ 9.5-10.5 mm, ♀ 9.5 mm; length of wing, ♂ 7.5 mm, ♀ 8 mm.

Type: Holotype ♀ in the Macleay Museum, Sydney.

Type locality: Kuranda, Queensland.

QUEENSLAND: Kuranda. NORTHERN TERRITORY: Brocks Creek, Burnside.

CERIOIDES MACLEAYI Ferguson

Plate 1, Fig. 16

Cerioides macleayi Ferguson, 1926*a*, Proc. Linn. Soc. N.S.W. **51**: 148.

Monoceromyia hardyi Shannon, 1927, J. Wash. Acad. Sci. **17**: 44.

Ferguson gave a full description of this species from a series of 4 males and 3 females. Shannon based his species *hardyi* on a single male specimen collected at the same place and time by the same collector (Brisbane, 12.xi.1912, H. Hacker) as one of the paratypes designated by Ferguson.

The following additional characters of the male are given. Hind trochanter with normal short hairs. Hind tibia not produced into a spine. Middle femur with the setae and hairs reduced. Middle tibia with an apical row of about 9 spines. Genitalia: aedeagus not hidden by the 4th abdominal sternite, quite short, only slightly exceeding the claspers. Claspers as long as broad at base, triangular in shape.

Size

Length of body, excluding antennifer, ♂ 9-9.5 mm, ♀ 11.5 mm; length of wing, ♂ 7-8 mm, ♀ 10 mm.

Types: In the Macleay Museum, Sydney.

Type locality: Rockhampton, Queensland.

QUEENSLAND: Rockhampton; Brisbane; Stanthorpe (2.xi.1927, S. M. Watson); Goondiwindi (29.xii.1927, F. H. Roberts); Westwood (20.xi.1927, A. P. Dodd); Southport (10.i.1930, H. Hacker); Chinchilla (Jan. 1924).

The species appears to be most closely allied to *atacta* though it differs strikingly in the male genitalia.

CERIOIDES DODDI Ferguson

Plate 1, Fig. 15

Cerioides doddi Ferguson, 1926*a*, Proc. Linn. Soc. N.S.W. **51**: 149.

Ferguson based his specific description on 2 females.

Type: In the South Australian Museum, Adelaide.

Type locality: Kuranda, Queensland.

This species is most closely allied to *macleayi* but it bears a superficial resemblance to *breviscapa.* In addition to the type I have examined a female specimen from the Cairns district.

CERIOIDES EUCHROMA, sp. nov.

Plate 1, Fig. 14

Male (holotype)

Face yellow, with a slight reddish median stripe and darker lateral margins to the face. Antennifer reddish brown, antennae somewhat darker, scape blackish. Vertex reddish in the median area, yellow laterad, black around the ocelli. Eyes touching for considerably more than ½ the distance between the ocelli and the base of the antennifer. Antennifer considerably longer than the 1st antennal segment, which is much longer than either the 2nd or 3rd; the last 2 segments are subequal in length. The style is quite short.

Thorax black, marked with yellow, finely granulose. Humeral angles, lateral margin extending back to the transverse suture, an irregular line from the transverse suture to the postero-lateral angle, a more or less circular area towards the midline just anterior to the scutellum, and scutellum, yellow. Mesopleural segments mostly yellow except ventrally. Legs reddish, yellowish at the joints, hind femora and tibiae darker. Hind trochanter with the normal short hairs. Hind tibia not produced into a spine. Middle femur with the setae and hairs reduced. Middle tibia with an apical row of 5 or 6 spines. Wings clear except for the dark brown anterior portion, bounded posteriorly in the basal ½ by the vena spuria and then by "R_{4+5}" to the wing margin, but not including the pronounced "dip" in that vein. Subcostal space clear.

Abdomen obviously and strongly contracted at base. First segment considerably wider than long, 2nd much longer than its greatest width, which is considerably less than that of the 1st. Distinct "waisting" of the abdomen at these basal segments. Third and 4th segments large, forming an ovate mass. First reddish brown, with the basal lateral margins yellow. Second darker reddish brown except for the yellow apex. Third reddish brown with narrow yellow apex. Fourth darker than the third and with a wider apical yellow band. Venter reddish brown except at the joints. Genitalia: aedeagus not hidden by the 4th abdominal sternite, quite short, only slightly exceeding the claspers, which are as long as broad at base, triangular in shape. Aedeagus noticeably, though slightly, longer than claspers.

Female

Similar in colouring to the male and with the abdomen slightly more bulbous.

Size

Length of body, excluding antennifer, ♂ 9.5 mm, ♀ 10 mm; length of wing, ♂ 7 mm, ♀ 7.5 mm.

Types: Holotype ♂ and allotype ♀ and 4 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Brocks Creek, Burnside, N.T. (Apr. 1929, T. G. Campbell).

This species is described from a series of 4 males and 2 females, all taken from the type locality. The species is similar to *macleayi* Ferguson but differs notably in the coloration of the 1st 2 abdominal segments.

CERIOIDES ALAPLICATA Hardy

Plate 2, Figs. 4, 5

Cerioides alaplicata Hardy, 1945*b*, Proc. Roy. Soc. Qd. **56**: 83.

Hardy has given a full description of this species, of which I have examined paratypes. The outstanding features are the sexual dimorphism in the length of the antennifer and the 2nd abdominal segment and the ability to fold the wings longitudinally. The species can be distinguished from *breviscapa* on the facial markings and the length of the antennifer.

Size

Length of body, excluding antennifer, ♂ 8-8.5 mm, ♀ 7.5-8 mm; length of wing, ♂ 7 mm, ♀ 6.5-7 mm.

Types: Holotype and allotype in Hardy collection.

Paratypes in various Australian collections, including Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Goondiwindi, Queensland.

QUEENSLAND: Goondiwindi (Nov. 1935, G. H. Hardy); Westwood (Oct. 1927, A. P. Dodd); Taroom (Dec. 1930, H. Hacker).

In addition to the paratypes, I have examined a male and a female from Westwood and a single female from Taroom, the latter differing from the typical form in the length of the antennifer, which, in the female, is only slightly longer than broad, and in the pigmentation of the wing, in which the subcostal space is without pigment. The scutellum has the whole of its surface reddish yellow, not just the posterior ½ as in typical *alaplicata*. The wing fold is present as in the typical form.

CERIOIDES BREVISCAPA (Saunders)

Plate 2, Fig. 3

Ceria breviscapa Saunders, 1845, Trans. Ent. Soc. Lond. **4**: 65.

Cerioides breviscapa Hardy, 1921, Aust. Zool. Sydney **2**: 13; Ferguson, 1926*a*, Proc. Linn. Soc. N.S.W. **51**: 148; Shannon, 1927, J. Wash. Acad. Sci. **17**: 42; Hardy, 1945*b*, Proc. Roy. Soc. Qd. **56**: 82.

Cerioides victoria Curran, 1925, Amer. Mus. Novit. **200**: 1.

Curran's description of *victoria* is almost identical with that given by Ferguson for *breviscapa* (Saunders) and the type locality for both species is Victoria. In pointing out this synonymy, Hardy observed that, though there was a slight deviation in each case from the original description, it was improbable that 2 closely related species of this group would be found in so southern a habitat.

Ferguson has given a description of both sexes, but does not mention the ability to fold the wings longitudinally. The following characters of the male are added: Hind trochanter with long hair. Hind tibia elongated into a definite spine on the ventral apical margin, that is, the margin apposed to the femur. Middle femur with a posterior fringe of long hairs, basal spines reduced. Middle tibia with an apical row of 5 or 6 spines. Genitalia: aedeagus not hidden by the 4th abdominal sternite. Aedeagus much longer than claspers, twice as long, tapering to a blunt point. Claspers as long as broad at base.

Size

Length of body, excluding antennifer, ♂ 8-9.5 mm, ♀ 9-10 mm; length of wing, ♂ 6.5-7.5 mm, ♀ 8-8.5 mm.

Type: In the British Museum.

Type locality: Port Phillip, Vic.

Distribution.—Victoria, New South Wales, South Australia, and Queensland.

The male specimen from Chinchilla, Queensland (Oct. 1927, A. P. Dodd) differs from those collected at Canberra in that the scutellum is almost completely black with the posterior border very dark reddish and the apical 1/3 of the 3rd abdominal segment is orange. In the Canberra specimens the scutellum is reddish brown and the 3rd abdominal segment has only a narrow yellowish or reddish apical border. The aedeagus of the Chinchilla specimen is considerably longer relatively than in the Canberra specimens. These differences probably indicate subspecific differentiation, but until more material is available they will be grouped together under *breviscapa.*

This species can be separated from all other Australian species except *phya* by the very short antennifer of both sexes. In this respect it is similar to the male of *alaplicata* but the female of that species has a distinct antennifer. The 2 species differ further in body coloration.

CERIOIDES PHYA, sp. nov.

Plate 1, Fig. 18

Female (holotype)

Face below antennifer dark, with a wide, oblique, yellow stripe on the cheek; a wide, transverse, yellow band enclosing the antennifer except below; antennifer and its base darker; vertex, behind ocelli, all reddish yellow to reddish brown, very small reddish patch anterior to median ocellus; antenna, including style, black. Eyes well separated, diverging strongly from the vertex. Antennifer very short, not ½ as long as the 1st antennal segment; 2nd and 3rd antennal segments of about equal length, much shorter than the 1st; style short, rather blunt.

Thorax black, finely granulose. Humeral angle reddish yellow, an area extending back to the transverse suture reddish brown. Scutellum evenly reddish brown. Remainder of thorax black. Legs black marked with yellow and reddish brown; fore and middle legs with apical ½ of femur and basal ½ of tibia reddish brown; hind leg with femur black except for reddish brown apex and tibia yellow over basal 1/3 or so. Wings infuscated over the anterior portion, more deeply so towards the apex. Wing folded longitudinally when at rest. Very little "dip" in the vein "R_{4+5}" but otherwise the venation normal with distinct cross vein from the end of Sc to R_1.

Abdomen strongly contracted at base; 1st segment short and narrowed from base to apex, 2nd short, only slightly longer than 1st, narrowing over its basal 1/3 and then expanding so that at its apex it is as wide as the 1st segment at base; remaining segments wide, 3rd very large, occupying more than ½ the rest of the abdomen, wider than succeeding segments; 1st completely black; 2nd black at base, passing through reddish brown to yellow at apex, black at meson limited to basal ¼ but extending to apical 1/3 laterally; 3rd segment black over basal ½ laterally and basal 2/3 at meson, grading through reddish brown to yellowish apex; 4th black with an even, reddish yellow, transverse band at apex; remaining segments dark.

Size

Length of body, excluding antennifer, ♀ 8.5 mm; length of wing ♀ 7 mm.

Type: Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: 100 miles W. Wanaaring, N.S.W. (30.x.1949, E. F. Riek), at flowers of *Atalaya hemiglauca.*

The species is described from the holotype. It differs from *breviscapa* mainly in the coloration of the head, but also of the legs and abdomen (segment 3).

THE FOLDING WINGS OF CERIOIDES BREVISCAPA (SAUNDERS) AND RELATED SPECIES

Some species of *Cerioides* are able to fold the wing longitudinally in certain positions of partial flexion. Five species, *breviscapa* (Saunders), *subarmata* Curran, *procapna* Riek, *phya* Riek, and *alaplicata* Hardy have this ability, but it is possible that other species with a petiolated abdomen will show this character. The ability to fold the wing is not known from the broad-abdomened species.

It is usually possible to tell from the pinned specimens whether a species folds the wings. Only 3 of the above species, *breviscapa, phya,* and *subarmata,* have been examined alive. The wing folding in the other two has been seen in the mounted specimens. The following discussion is based mainly on *breviscapa* though *subarmata* and *phya* behave similarly.

The completed fold is formed by two negative creases, one lying close behind the media and the other behind 1*A*. In examining the fold from the base to the apex of the wing one finds that it follows first the anal crease to about the middle of the alula. Then it bends across to the median crease, though in the intermediate area it still follows the anal crease which is bent away from the line of its basal part by torsion of the wing membrane brought about by the stronger median crease. Then the fold follows the median crease to the wing margin.

The anal crease itself continues to the wing margin but decreases in strength as it proceeds towards that margin. The median crease likewise is continued somewhat towards the base of the wing, more basad than the point of cross-over from the anal crease. When viewed from above these continuations of the creases are not included in the actual line of folding.

The fold is most definite at the base of the wing with the posterior portion of the wing lying close above the anterior, forming a distinct V in cross section, the arms of the V almost touching. As one follows the fold towards the wing margin there is a decrease in the strength of the fold so that at the wing margin itself the cross section is ⊔-shaped, the angles being formed by the anal and median creases which are somewhat rounded off so that there is a tendency towards the U shape.

When viewed from behind the folded wing presents a triangular area bounded by the anal and median creases with only the veins M_{3+4} and Cu visible.

As outlined above, in these species, instead of the normal negative anal fold of *Cerioides,* there is a composite fold combining both the negative anal and median folds. This development of the median fold can be explained by the proportionate development of the basal sclerites or axillaries articulating the wing to the thorax. If it were possible for the median crease to continue to the base of the wing across the arculus then the anal fold would not be necessary to produce a folded wing. In all species of *Cerioides* which have been examined there is a complete anal fold, different to the folded alula normal for Diptera, indicating possibly that they have all progressed towards wing folding but the folding has been completed only in a few species.

The negative median fold of the wing in *Cerioides* is not associated in any way with the positive vena spuria, which lies between the radius and the media, whereas the crease or fold lies behind the media and passes across its posterior branch forming a definite break in the vein.

The folding of the wing in the living fly is automatic, depending only on the position of the wing, that is, the angle it makes with the body of the insect. When the wings are fully extended they are flat, as one would expect for flight. When the fly alights the wings may assume one of two positions, either that of rest or the alert position. In the alert position the wings are held at an angle of about 45° to the abdomen and then the wings are folded longitudinally. In the position of rest the wings lie dorsally along the abdomen with one slightly overlapping the other and then the wings are flat. In the rotation from the flexed to the extended position, an angle of 90° or so, the wing passes from flat to folded and then back to flat again. The amount of folding is dependent on the position of the wing relative to the longitudinal axis of the body so that every degree of folding is assumed in the rotation from flexed to extended. The wing is not flat for most of the rotation and sharply folded at a given point.

It is possible for the fly to fold one wing while the other remains flat in the position of rest. The same also applies to the vibrating of the wings, one wing can be vibrated and so flattened while the other remains stationary, folded in the alert position. It is difficult to understand the muscle reaction which would produce this condition but the flexing of the wing apparently prevents the action of the indirect wing muscles on the given wing.

The Mechanism of Folding

In flexion from the fully extended position the third axillary is drawn upwards and in towards the body. In doing so it comes in contact with one of the median plates, rotating this backwards so that its outer extremity abuts against the anterior projection from the base of 1*A*, forcing this portion down and back. The corresponding posterior projection is forced up and over so that, with the slight backward movement of the fore part of the wing, it comes to pass beyond vertical to the plane of this anterior portion. This forces the hind half of the wing forward over the anterior half.

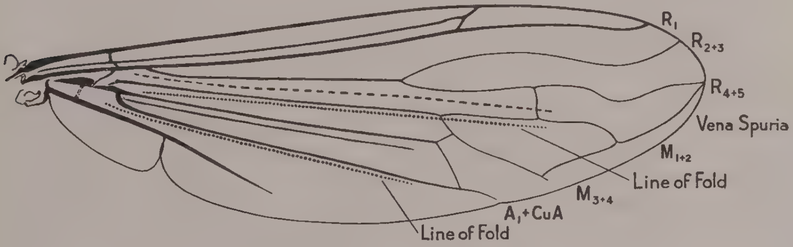

Fig. 1.—Wing of *Cerioides breviscapa* (Saunders), showing the lines of folding. × 7.5.

With further flexion the upper end of the third axillary moves in towards the body and somewhat backwards, carrying the articulating base of 1*A* with it. As the third axillary moves through a distance relatively great compared with the first and second axillaries, the anterior and posterior projections at the base of *A* come to occupy a horizontal position again, as in the extended wing, and the wing fold opens, flattening the wing.

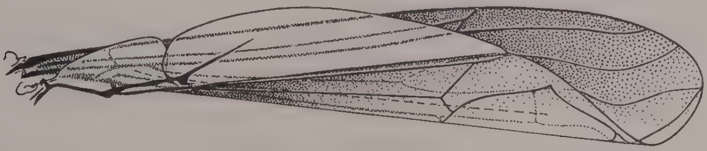

Fig. 2.—The folded wing of *Cerioides breviscapa*. × 7.5.

Comparison with the Wing Folding of Certain Hymenoptera

The folding of the wing in *Cerioides* (Figs. 1, 2) differs strikingly from that of its "mimic" model, the vespoid Hymenoptera (Fig. 4). In these Hymenoptera and also in the Leucospidinae of the Chalcididae (Fig. 3) and other small families the fold of the fore wing is a positive one which does not pass to the wing base but cuts through the hind margin close to the base.

Such folding seems to be controlled in the freshly emerged wasp by the wing coupling apparatus, which in these groups is more definite than in some other types. When the wings are flexed the coupling remains intact so that as the fore wing rotates back over the hind wing it must fold, its hind margin coming to lie under its fore margin and above the hind wing, thus producing a positive fold in the fore wing.

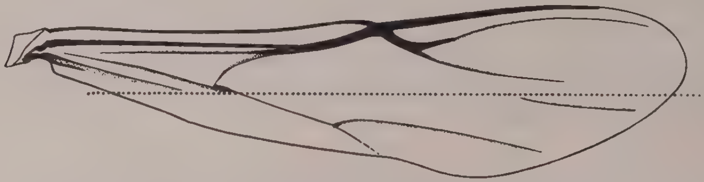

Fig. 3.—Fore wing of the chalcidoid *Exoclaenoides mutilloides* Girault, showing the line of folding. × 7.5.

In the pupa there is no folding of the wing membrane which, in this respect, is similar to that of other Hymenoptera. After hardening in the adult state the wing will fold when the coupling to the hind wing is broken, whether the wing be flexed or extended, so that without coupling of the two wings it is not possible for the wasp to fly efficiently. If the hind wing is removed from an adult before it emerges from the pupal cell or if its wing coupling apparatus is removed, then, when the wing membrane hardens, there will be no folding of the fore wing, but it will remain flat in all positions of flexion and extension. This indicates that the folding is induced by the strong coupling of the two wings.

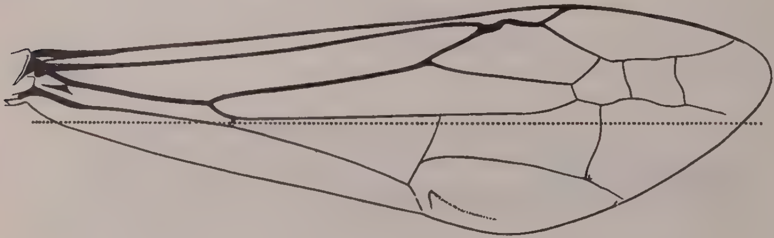

Fig. 4.—Fore wing of the vespoid *Polistes variabilis* Sauss., showing the line of folding. × 5.

In the Hymenoptera the degree of folding increases the more the wings are flexed until it is greatest in the position of rest. This is very different to that seen in *Cerioides.*

ACKNOWLEDGMENTS

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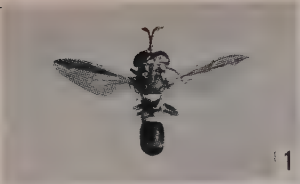
AUSTRALIAN CERIOIDINAE (DIPTERA)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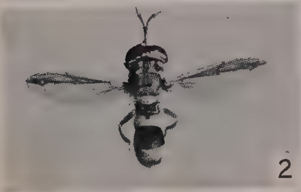
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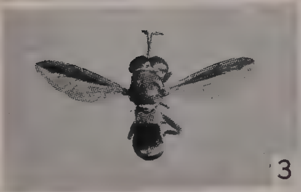
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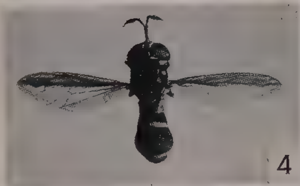
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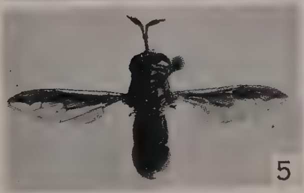
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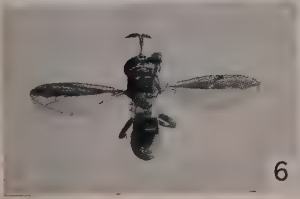
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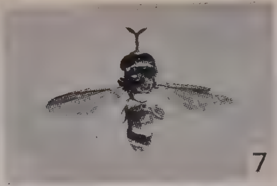
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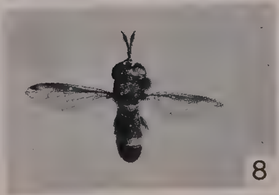
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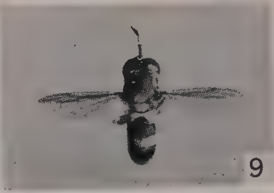
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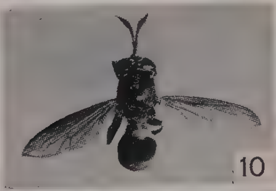
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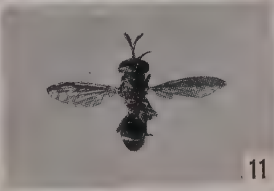
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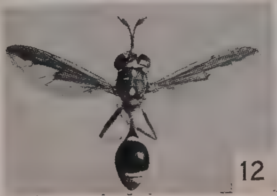
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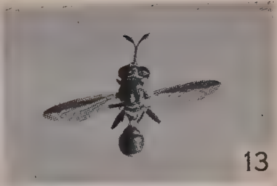
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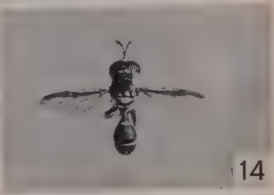
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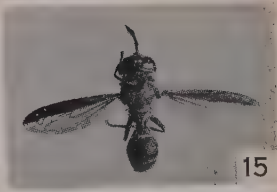
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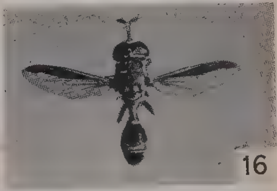
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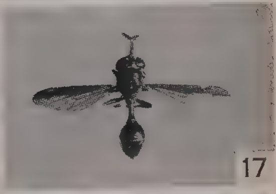
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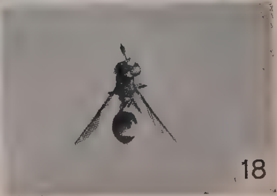
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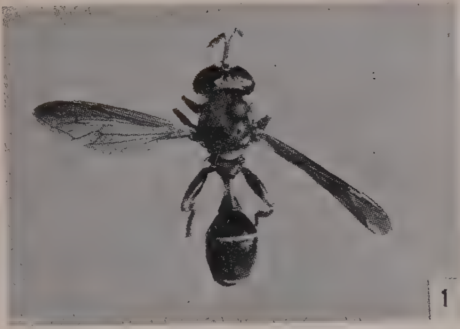
PLATE 2



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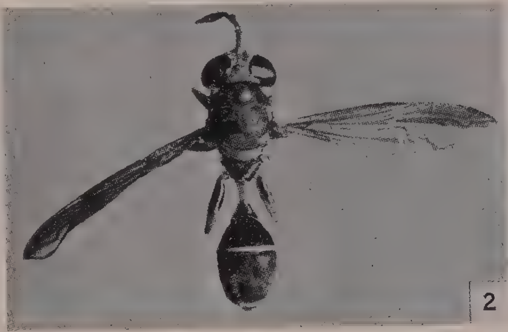

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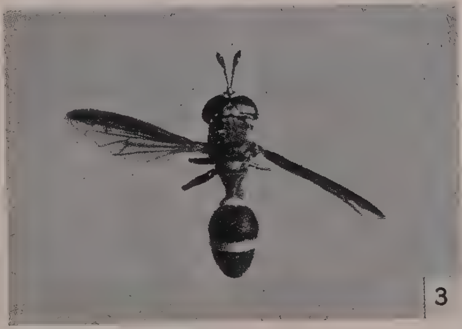

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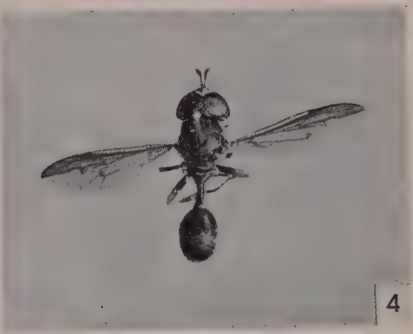

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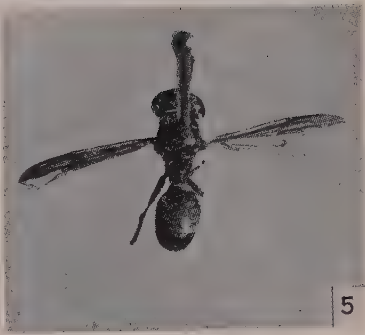

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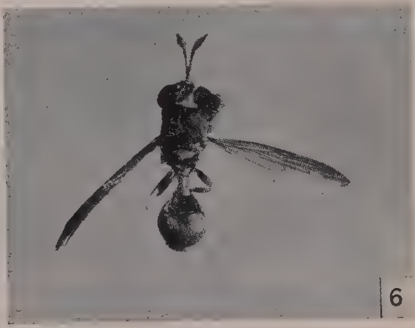

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done by Mr. L. A. Marshall, Division of Entomology, C.S.I.R.O. Figures 1-4 were prepared by Mr. L. A. Marshall from outline drawings by the author. I am most grateful for their assistance.

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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—*Cerioides ornata* (Saunders), ♂, Brocks Creek, N.T. Natural size.
Fig. 2.—*Cerioides ornata australis* (Macquart), ♂, Canberra, A.C.T. Natural size.
Fig. 3.—*Cerioides euphara*, nom. nov., ♂, Eidsvold, Queensland. Natural size.
Fig. 4.—*Cerioides alboseta* Ferguson, ♀, Kuranda, Queensland. Natural size.
Fig. 5.—*Cerioides apicalis* Ferguson, ♀, allotype, Goondiwindi, Queensland. Natural size.
Fig. 6.—*Cerioides sphenotoma*, sp. nov., ♀, holotype, Chinchilla, Queensland. Natural size.
Fig. 7.—*Cerioides lypra*, sp. nov., ♂, holotype, Bathurst I., N.T. Natural size.
Fig. 8.—*Cerioides opuntiae* Ferguson, ♀, allotype, Cuttebrai Creek, N.S.W. Natural size.
Fig. 9.—*Cerioides picta*, sp. nov., ♂, holotype, G'bluie, N.S.W. Natural size.
Fig. 10.—*Cerioides optata*, sp. nov., ♀, holotype, Australia. Natural size.
Fig. 11.—*Cerioides mastersi* Ferguson, ♂, Brisbane, Queensland. Natural size.
Fig. 12.—*Cerioides tolmera*, sp. nov., ♀, allotype, Cotter River, A.C.T. Natural size.
Fig. 13.—*Cerioides atacta*, nom. nov., ♀, Brocks Creek, N.T. Natural size.
Fig. 14.—*Cerioides euchroma*, sp. nov., ♂, holotype, Brocks Creek, N.T. Natural size.
Fig. 15.—*Cerioides doddi* Ferguson, ♀, Cairns district, Queensland. Natural size.
Fig. 16.—*Cerioides macleayi* Ferguson, ♂, Collinsville, Queensland. Natural size.
Fig. 17.—*Cerioides ablepta*, sp. nov., ♀, holotype, National Park, N.S.W. Natural size.
Fig. 18.—*Cerioides phya*, sp. nov., ♀, holotype, Wanaaring, N.S.W. Natural size.

Plate 2

Fig. 1.—*Cerioides subarmata* Curran, ♂, Sunnybank, Queensland, showing folded wing. × 3.
Fig. 2.—*Cerioides subarmata* Curran, ♀, allotype, Sunnybank, Queensland, showing folded wing. × 3.

Fig. 3.—*Cerioides breviscapa* (Saunders), ♂, Canberra, A.C.T., showing folded wing. × 3.

Fig. 4.—*Cerioides alaplicata* Hardy, ♂, Westwood, Queensland. × 3.

Fig. 5.—*Cerioides alaplicata* Hardy, ♀, paratype, Goondiwindi, Queensland, showing folded wing. × 3.

Fig. 6.—*Cerioides procapna*, sp. nov., ♀, holotype, Eidsvold, Queensland, showing folded wing. × 3.

LIST OF SPECIES

Genus *Cerioides*

C. ablepta, sp. nov. 119
C. alaplicata Hardy 123
C. alboseta Ferguson 108
C. apicalis Ferguson 109
C. atacta, nom. nov. 120
C. breviscapa (Saunders) 123
C. doddi Ferguson 121
C. euchroma, sp. nov. 122
C. euphara, nom. nov. 107
C. lypra, sp. nov. 111
C. macleayi Ferguson 121
C. mastersi Ferguson 115
C. mellivora (Shannon) 107
C. optata, sp. nov. 114
C. opuntiae Ferguson 112
C. ornata (Saunders) 104
C. ornata australis (Macquart) .. 106
C. phya, sp. nov. 124
C. picta, sp. nov. 113
C. platypus Ferguson 109
C. procapna, sp. nov. 118
C. saundersi (Shannon) 106
C. sphenotoma, sp. nov. 110
C. subarmata Curran 117
C. tolmera, sp. nov. 116

THE AUSTRALIAN MEGALOPTERA OR ALDER-FLIES

By E. F. Riek*

[*Manuscript received September* 10, 1953]

Contents

Summary 131
Introduction 131
Systematics 132
Family Corydalidae 132
Key to Australian genera and species of the family Corydalidae 132
Genus *Archichauliodes* 133
Genus *Austrochauliodes* 137
Family Sialidae 138
Genus *Austrosialis* 139
Acknowledgments 141
References 141
List of species 142

Summary

The paper deals with the systematics of all known Australian Megaloptera. One new species, *Archichauliodes anagaurus*, and two new subspecies, *A. guttiferus guttiferus* and *A. g. polypastus*, are described.

Introduction

The families Corydalidae and Sialidae both occur in the Australian region, two species of the former and three of the latter having been described. The corydalids, though widespread, are not well represented in collections. The adults are more or less nocturnal and are taken on the wing only at dusk and early twilight, except when newly emerged from the pupa or on dull days. Occasionally a female will be observed on the wing during the day in a shaded portion of a stream. The Australian sialids are even less known and are generally collected by sweeping along streams. Occasionally both sialids and corydalids are attracted to light.

The only recorded Australian Corydalidae are *Hermes dubitatus* and *H. guttiferus* of Walker (1853). The species *dubitatus*, described without locality, is common in the coastal areas of Queensland and New South Wales; *guttiferus*, a well-known form, has been confused with a number of other Australian species, even including *dubitatus*, which is generically district. Since Walker's paper, separation of the species of Australian Corydalidae has not been attempted. Tillyard (1919) remarked on the striking variation in size and coloration but was content to group all the forms under the one species, *Archi-*

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chauliodes guttiferus (Walker). Kimmins (1938) has discussed *dubitatus* but considered it a South American species which he placed in *Protochauliodes.*

Tillyard (1919) described two sialids (each from unique specimens), which he placed in distinct genera. Lestage (1930) dealt in some detail with further specimens of the Tasmanian *Austrosialis ignicollis* Tillyard. Navas (1927) described *Protosialis australis,* which is a synonym of *Austrosialis australiensis* (Tillyard).

The present paper deals with the Corydalidae, which fall naturally into two genera, one monotypic for *dubitatus* Walker, occurring along the coastal areas of Queensland and New South Wales, and the second more widespread, with at least two Australian species, one of which (*guttiferus*) is divisible into definite subspecies. The sialid, *Austrosialis australiensis* (Tillyard), is described from a series of nine specimens including both sexes, but material of the second species (*A. ignicollis* Tillyard) has not been examined.

In addition to adult material, the larval stages of all species of the Corydalidae are known and their characters are included in the specific descriptions.

SYSTEMATICS

Order MEGALOPTERA

The order is conveniently divided into two families, the Corydalidae of medium to large size and the Sialidae all of rather small size.

Three ocelli; 4th tarsal segment simple, not bilobed; insects of medium to large size; aquatic larva with 8 pairs of lateral abdominal gills . . . . Family Corydalidae

Ocelli wanting; 4th tarsal segment prominently bilobed; insects of rather small size; aquatic larva with 7 pairs of lateral abdominal gills . . . . Family Sialidae

Family CORYDALIDAE

The family is generally divided into two subfamilies on a combination of wing structure and male genitalia, but one or two exotic species seem to occupy an intermediate position, having the genitalia of one group and the wing venation of the other.

Male with a pair of appendices superiores and inferiores; wing with more than 3 cross veins between *R* and *Rs*; head quadrangular, with a more or less developed tooth at the sides; large forms . . . . Corydalinae

Male with only a pair of appendices superiores; wings always with 3 cross veins between *R* and *Rs*; head triangular, no tooth at the sides, medium to large forms . . . . Chauliodinae

All the Australian species belong to the subfamily Chauliodinae with only three cross veins between *R* and *Rs.*

KEY TO AUSTRALIAN GENERA AND SPECIES OF THE FAMILY CORYDALIDAE

Adults

1. Vein 2*A* of fore wing fused to 1*A* for part of its length. . *Austrochauliodes,* gen. nov.
   *Rs** of 4 branches; no well-developed spots on hind wing . . . .
   Austro. dubitatus (Walker)
   Vein 2*A* of fore wing connected to 1*A* by a cross vein. *Archichauliodes* Weele 2

* *MA* is fused to *Rs.* See Figure 2 for venational scheme adopted.

2 (1). Hind wing without pignent spots; *Rs* 5- or 6-branched. . *Archi. anagaurus,* sp. nov.
Hind wing with 4 or 5 definite pigment spots. *Archi. guttiferus* (Walker) 3
3 (2). Fore wing with isolated spots . . . . *Archi. guttiferus guttiferus* (Walker)
Fore wing with more diffuse pigmentation tending to transverse banding . . . . *Archi. guttiferus polypastus,* subsp. nov.
Diffuse pigmentation on both fore and hind wings . . . . *Archi. guttiferus phaeoscius,* subsp. nov.

Larvae

1. Flagellum of antenna (3rd and 4th segments) much shorter than 2nd segment . . . . *Austrochauliodes*
Posterior tooth of mandible larger than median; posterior spiracle not raised on a distinct stalk; prothorax and head densely clothed in setae . . . . *Austro. dubitatus*
Flagellum of antenna as long as or longer than 2nd segment. Prothorax and head almost free of setae. *Archichauliodes* 2
2 (1). Posterior spiracle raised on a long stalk. Posterior tooth of mandible smaller than median; prothorax slightly wider than long . . . . *Archi. guttiferus*
Posterior spiracle not raised on a stalk 3
3 (2). Prothorax transverse (broader than long); gular plate with antero-lateral portion wide . . . . *Archi. anagaurus*
Prothorax longer than broad; gular plate with antero-lateral portion narrowed (New Zealand) . . . . *Archi. diversus* (Walker)[*]

Genus ARCHICHAULIODES Weele

Archichauliodes Weele, 1909, Notes Leyden Mus. **30**: 257.

Genotype *Hermes diversus* Walker, 1853 (= *Archichauliodes dubitatus* Weele, 1909 partim, non Walker).

Adult with *2A* of fore wing connected to vein *1A* by a cross vein, not fused with it for part of its length. The 1st radial cross vein is directed basally. *Rs* pectinately branched, *M* 2-branched (M_{1+2} and M_{3+4}), *CuA* forked. In the hind wing M_{1+2} is simple as in the fore wing. The genus is very similar to the South African *Platychauliodes*, but differs in the direction of the 1st radial cross vein.

Larva with flagellum of antenna as long as or longer than the 2nd segment. Posterior spiracle either raised on a stalk or sessile. Prothorax transverse or longer than broad. Head and prothorax almost free of setae.

ARCHICHAULIODES GUTTIFERUS (Walker)

Fig. 1

Hermes guttiferus Walker, 1853, List Neuropt. Ins. Brit. Mus. **2**: 204.

Achichauliodes guttiferus Weele, 1910, Coll. Selys. **5**: 48; Kimmins, 1938, Ann. Mag. Nat. Hist. (11) **2**: 358.

Walker originally described this species as follows: "Obscure ferrugineus; alae subcinereae, anticae fusco guttatae, posticae fusco trimaculatae.

"Body dark ferruginous; head broader in front with some longitudinal ridges on the disc, a little broader and longer than the prothorax, eyes slightly prominent; prothorax a little impressed on each side, with a slight longitudinal furrow, much longer than broad, wings slightly grey, forewings adorned with very numerous brown dots of various size between all the veins and with two brown spots towards the tip of the fore border; marginal region with about 28 transverse veins, hindwings with three large brown spots, one adjoining the marginal region, the second on the fore border, between the first and third, which is in the disc. Length of the body 10? lines; of the wings 32 lines."

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[*] See Plate 1, Figure 4.

In the above description Walker mentions only 3 large spots on the hind wings. A 4th is usually well developed. In some specimens 5 spots are clearly defined but the 2 situated between *MA* and *M*, and the apical spot, are the most constant. The 2 sexes differ in the size and shape of the wings. The fore wing shows pronounced variation in the different subspecies. Male genitalia described for the different subspecies differ strikingly.

Wing venation: Vein *2A* connected to *1A* by a cross vein. *Rs* 6-branched but occasionally only 5-branched. *M* of fore wing 2-branched, of the hind wing typically 2-branched but occasionally with 3 branches (M_{1+2} dividing into M_1 and M_2).

Distribution.—Coastal regions of New South Wales, Queensland, and Victoria.

This species can be divided into 3 well-marked subspecies on the combination of male genitalia and pigmentation of the wing.

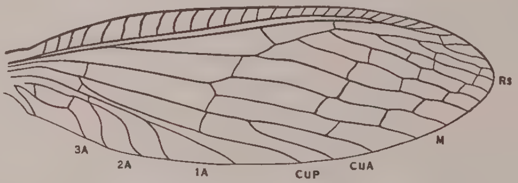


Fig. 1.—*Archichauliodes guttiferus* (Walker). Fore wing. × 2⅛.

Archichauliodes guttiferus guttiferus (Walker)

Plate 1, Fig. 1

In the typical subspecies there are generally 4 large spots on the hind wing; the 1st 2 are situated between *MA* and *M*, one just before the furcation of *MA* and *Rs*, the other equidistant between the wing margin and the 1st; the 3rd and 4th spots are situated along the costal margin, the former, more basal, one in the area bounded by the 1st and 2nd radial cross veins, the latter towards the apex of the wing. Generally there are distinct fine spots at the apex of the wing but these are most variable. The fore wing is covered with numerous isolated black spots, with 2 larger ones along the costal margin in the apical 1/3 of the wing. Occasionally there is a tendency to blotching rather than spotting.

Genital appendages of male relatively long and thin, slightly incurved at apex, basal 1/3 rather more stout and then narrowed suddenly before tapering gradually to the apex; latero-basal callosity ("sensory spot") only slightly developed, circular in lateral aspect. Ninth abdominal segment with posterior margin slightly excavate in its central portion, anterior margin concave. Terminalia of female short and bluntly tapered, outer circular "sensory spot" almost at middle of the length of the appendage and only slightly raised.

Type: In the British Museum.

Type locality: Australia.

NEW SOUTH WALES: Sydney; Blue Mountains. A.C.T.: A long series of bred material from the Cotter River, near Canberra. VICTORIA: Smeaton.

ARCHICHAULIODES GUTTIFERUS POLYPASTUS, subsp. nov.

Plate 1, Fig. 2

The hind wing has either 4 or 5 spots. When a 5th spot is present it lies on the cross vein connecting *CuA* and *CuP*. Occasionally the more basad spot of the costal margin is lacking but then the 5th spot described above is present. These spots are considerably smaller than in the typical form. Apex of the wing normally with a number of distinct fine spots. Fore wing with numerous spots, tending to merge so as to produce a slight transverse banding of the wing, this banding being most obvious in the region of the 2 larger marginal spots.

Genital appendages of the male very short and stout, apex strongly incurved. The basal ½ of the appendage has almost parallel sides and thence tapers somewhat, at the same time curving inwards, to the rounded apex. Latero-basal callosity ("sensory spot") very prominent, particularly in lateral view, when it appears almost circular. Ninth abdominal segment with posterior margin almost straight except for the sloping sides, anterior margin deeply concave. Terminalia of female almost straight, shorter and more rapidly tapered than in typical form, outer circular "sensory spot" larger and more strongly developed.

Types: Holotype ♂, allotype ♀, and paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Binna Burra, Lamington National Park, Queensland.

ARCHICHAULIODES GUTTIFERUS PHAEOSCIUS, subsp. nov.

Plate 1, Fig. 3

The hind wing has the 4 spots of the typical form but those of the costal margin have merged. The apical ½ of the wing shows an irregular blotching with almost complete pigmentation. Fore wing densely covered with spots and blotches, more deeply pigmented in the apical ½, where there is a slight transverse banding.

Genital appendages of male long and thin, with a distinct ventral curvature, tapering rather gradually to the blunt apex except in the middle, where it tapers rather rapidly. Latero-basal callosity ("sensory spot") small but sharply demarcated from the rest of the appendage, tending to be spherical. Ninth abdominal segment with posterior margin almost straight except for the forwardly sloping sides; anterior margin straight.

Types: Holotype ♂ in the Division of Entomology Museum, C.S.I.R.O., Canberra. Paratype ♂ in the Queensland Museum, Brisbane.

Type locality: Cairns district, Queensland.

Larvae of guttiferus.—It is almost impossible to separate the larvae of the 3 subspecies, though *phaeoscius* shows a slightly more elongated stalk for the posterior spiracles. Antenna long, with the flagellum (3rd and 4th segments) as long as or longer than the 2nd segment. Posterior pair of spiracles each raised on a long stalk, recalling the siphon of a mosquito larva. Surface of head and prothorax almost free of setae. Posterior tooth of the mandible smaller than the median one. Prothorax almost square in outline but slightly wider than long.

ARCHICHAULIODES ANAGAURUS, sp. nov.

Plate 1, Figs. 7, 8

The almost complete lack of pigmentation over the membrane of the hind wing distinguishes this species. Fore wing with irregular scattered mottlings more pronounced in the costal region, particularly towards the apex; these mottlings tend to a transverse banding similar to that of *diversus* of New Zealand but are not so pronounced. Hind wing without spots or mottlings except in the costal region and there limited to the apical ½. There are, however, 2 small isolated spots lying between *MA* and *M* and corresponding to 2 of those seen in *guttiferus*.

Wing venation very similar to that of *A. guttiferus* but *Rs* typically 5-branched, rarely showing a 6-branched condition in some of the paratypes.

Genital appendage of the male short and stout, without decided ventral curvature, tapering only slightly to the rounded apex. Basal ½ with parallel sides and then the appendage curves slightly outwards so that the inner faces of the pair are slightly flattened and apposed. Latero-basal "sensory spot" slightly raised. Ninth abdominal segment with posterior margin slightly excavated, anterior margin straight. Eighth segment also slightly sclerotized in some paratype specimens. Terminalia of female long and thin, basal ½ stout, apical ½ very thin, "sensory spot" quite prominent, occupying the apical portion of the basal ½ of the appendage.

Type: Holotype ♂, allotype ♀, and 3 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra. Six ♀♀ paratypes, all from Mt. Kosciusko, in the Australian Museum, Sydney.

Type locality: Mt. Kosciusko, N.S.W., ♂, 2.i.1930; ♀, 17.xi.1938.

NEW SOUTH WALES: Mt. Kosciusko region. VICTORIA: Big River.

Larva.—Antenna long, with the flagellum as long as or longer than the 2nd segment. Posterior pair of spiracles not raised on a definite stalk as in *guttiferus*. Surface of head and prothorax almost free of setae. Posterior tooth of mandible larger than median tooth. Prothorax slightly broader than long. The larvae of this species can be separated from those of the New Zealand *diversus*, which also have short posterior spiracles, on the structure of the prothorax and the shape of the gular plate.

Genus AUSTROCHAULIODES, gen. nov.

Genotype *Hermes dubitatus* Walker, 1853.

Vein 2*A* of fore wing fused to 1*A* for part of its length; 1st radial cross vein directed towards the anterior margin or slightly apically; *Rs* branching dichotomously, not pectinately; M_{1+2} typically simple but occasionally forked; *CuA* forked. In the hind wing M_{1+2} forks into M_1 and M_2, and M_{3+4} rarely divides into M_3 and M_4.

The genus resembles the South African *Taeniochauliodes* in the structure of the anal veins but differs in the 1st radial cross vein, in its dichotomously branched *Rs*, and in the forked condition of M_{1+2} of the hind wing. It differs from the South American *Protochauliodes* in the structure of the male genitalia. In *Austrochauliodes* the appendices superiores are long and straight, while in *Protochauliodes* they are truncate or slightly bifurcate at the apex. The wing venation of *Protochauliodes* differs slightly from that of *Austrochauliodes*, the 1st radial cross vein being directed basally whereas in *Austrochauliodes* it is directed towards the anterior margin. *Austrochauliodes* can be distinguished from *Archichauliodes* on the structure of the anal veins of the fore wing and the forked M_{1+2} of the hind wing.

Larva.—Flagellum of antenna very short, much shorter than the 2nd segment. Head and prothorax densely clothed with setae. In *dubitatus*, the only species of the genus, the posterior spiracles are not raised on definite stalks and the posterior tooth of the mandible is larger than the median.

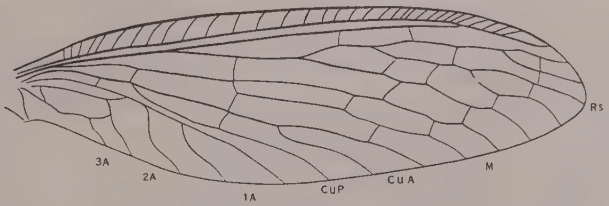


Fig. 2.—*Austrochauliodes dubitatus* (Walker). Fore wing. × 2-1/5.

AUSTROCHAULIODES DUBITATUS (Walker)

Fig. 2; Plate 1, Figs. 5, 6

Hermes dubitatus Walker, 1853, List. Neuropt. Ins. Brit. Mus. **2**: 204.
Chauliodes californicus McLachlan, 1867 partim, non Walker, J. Linn. Soc. (Zool.) **9**: 260.
Chauliodes diversus McLachlan, 1869 partim, non Walker, Ann. Mag. Nat. Hist. (4) **4**: 37.
Archichauliodes dubitatus Weele, 1910 partim, Coll. Selys. **5**: 46.
Protochauliodes dubitatus Kimmins, 1938, Ann. Mag. Nat. Hist. (11) **2**: 356.

Kimmins (1938) has examined the types of *Hermes dubitatus* Walker and *Hermes diversus* Walker in the British Museum and his examination shows that they are generically distinct. Previous workers had regarded them as synonyms, giving priority to *dubitatus* and referring this species to the New Zealand fauna. This species is known only from the type female, which is without locality data.

Previously it was regarded as a New Zealand species, but Kimmins considered it as South American; whereas a comparison of specimens with the photographic plate given by Kimmins shows that it is really an Australian species, occurring from the costal region of south-eastern Queensland to as far south as Sydney.

The hind wing is without definite spots, except towards the apex, but is covered with a fine speckling. The spots are more or less isolated in the female but merge in the male. In both sexes there is a clear transverse band separating the apical and middle thirds of the wing. Fore wing more deeply pigmented than the hind and with the sexual differences more pronounced. In the female the wing is covered with numerous isolated spots showing a tendency to transverse banding. In the male the pigmentation is more general, with the apical ½ of the wing almost completely pigmented except for the clear transverse band corresponding to that seen in the hind wing. This band is also present in the female fore wing.

Wing venation: *2A* of the fore wing fused to *1A* for part of its length. *Rs* 4-branched, rarely with a fine additional terminal branching. *M* of fore wing typically of 2 branches; in the hind wing with at least M_{1+2} dividing into M_1 and M_2. In the hind wing *2A* is connected to *1A* by a cross vein similar to that seen in *Archichauliodes.*

Wing span 70-80 mm. The species is slightly larger than *Archichauliodes guttiferus* (Walker) and does not show the marked difference of size and shape between the sexes, although the pigmentation is very distinctive.

Genital appendage of the male short and stout, with a definite, though slight, ventral curvature, tapering to a sharp but rounded apex. On the inner side of the basal ½ there is a prominent swelling occupying almost ½ the length of the appendage and on which the hairs are absent, though it is covered with fine setae. Latero-basal callosity ("sensory spot") not sharply demarcate and only slightly raised. Terminalia of the female rather short and stout, tapering evenly almost to the apex, which is more or less cylindrical.

Type: Holotype ♀ in the British Museum.

Type locality: The type is without locality data.

QUEENSLAND: Lamington National Park; Bunya Mountains; Mt. Tambourine. NEW SOUTH WALES: Blackheath; Stanwell Park; Sydney.

Larva.—Flagellum of antenna much shorter than the 2nd segment. Head and prothorax densely clothed in setae. Posterior spiracles not raised on definite stalks. Posterior tooth of mandible larger than median. Prothorax transverse, slightly broader than long. The larvae of this species can be separated from those of *Archichauliodes anagaurus*, which also have short posterior spiracles, on the antennae and the setae of the head and prothorax.

Family **SIALIDAE**

The sialids are of small size and, though divided into a number of generic types, rather similar in appearance. The Australian forms are longer and thinner than the typical *Sialis*. Three generic names have been applied to the species, 2 by Tillyard and 1 by Navas. The 2 valid species are considered to belong to the 1 genus.

Genus AUSTROSIALIS Tillyard

Austrosialis Tillyard, 1919, Proc. Linn. Soc. N.S.W. **43** (4): 823.
Stenosialis Tillyard, 1919, Proc. Linn. Soc. N.S.W. **43** (4): 824.
Protosialis Navas, 1927 (partim), Broteria, Zool. **24**: 28.
Austrosialis Lestage, 1930, Bull. Soc. Ent. Belg. **70**: 109.

Genotype *Austrosialis ignicollis* Tillyard, 1919.

Lestage (1930) has recorded the inaccuracies of, and variation from, the description of the genotypic species given by Tillyard (1919). Tillyard described 2 species, each from unique specimens, which he placed in distinct genera, differing from one another only in the relative width of the costal field. The other recorded differences are inaccuracies of description due partly to the poor specimen of *australiensis.* Although Tillyard regarded the specimen of each species as probably a female, it is considered that that of *ignicollis* is a male. Both male and female specimens of *australiensis* are known and in that species the costal space of the male is relatively wider than that of the female. The wing, in general, is shorter and broader in the male.

Generic diagnosis.—Fore wing with the costal space broadened, particularly in the male, and with a variable number of veinlets, which become less pronounced and more oblique towards the apex of the wing. *Rs* dividing into R_2, R_3, R_4, and R_5, each of which is simple, not showing secondary branching. Three cross veins between *R* and *Rs*. M_{1+2} and M_{3+4} each forked. *CuA* forked, *CuP* simple. 1*A* simple, 2*A* forked and connected to 1*A* by a cross vein, 3*A* simple and connected to 2*A* by a cross vein. Hind wing with the costal space typically narrow, generally with less veinlets than fore wing. R_{2+3} and R_{4+5} branching into the component veins. M_{1+2} forked but M_{3+4} simple. Cubital and anal veins very similar to those of the fore wing. Genitalia of the male consisting only of the short appendices superiores.

The genus differs from *Leptosialis* of South Africa in the branching of *Rs* and of *M* of both wings. In the fore wing of *Leptosialis Rs* forks only into R_2, R_3, and R_{4+5}; *M* has only 2 branches. In the hind wing *Rs* and *M* show branching similar to that of the fore wing. *Austrosialis* shows branching of *Rs* similar to that of *Protosialis* but differs in the 4-branched condition of *M* in the fore wing (in *Protosialis* M_{1+2} is simple). In the hind wing M_{1+2} and M_{3+4} are both simple in *Protosialis,* whereas M_{1+2} forks in *Austrosialis.*

AUSTROSIALIS IGNICOLLIS Tillyard

Austrosialis ignicollis Tillyard, 1919, Proc. Linn. Soc. N.S.W. **43** (4): 823; Lestage, 1930, Bull. Soc. Ent. Belg. **70**: 109.

This species was figured by Tillyard but the wing venation is considered by Lestage (who examined 3 additional specimens) to be inaccurate in some respects, particularly with regard to 3*A* and the basal cross vein between *M* and *Cu* in the fore wing.

Type: In Tillyard collection, British Museum.

Type locality: Maria I., east coast of Tasmania, 29.xii.1915 (G. H. Hardy).

Also recorded from Eaglehawk Neck, Tas., by Lestage.

I have not examined specimens of this species, which very probably is limited to Tasmania. The species is distinguishable from *australiensis* mainly on the coloration and ornamentation of the head and prothorax and also on minor differences in the venation.

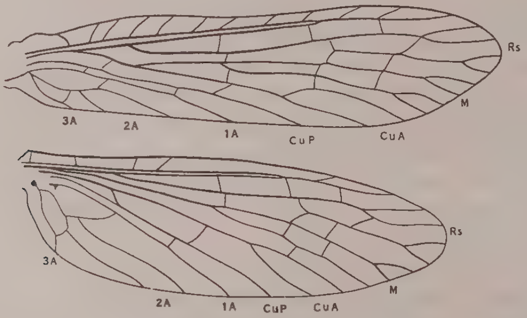


Fig. 3.—*Austrosialis australiensis* (Tillyard). Wings, female. × 6-2/3.

AUSTROSIALIS AUSTRALIENSIS (Tillyard)

Fig. 3; Plate 1, Fig. 9

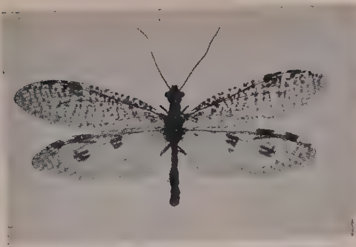
Stenosialis australiensis Tillyard, 1919, Proc. Linn. Soc. N.S.W. **43** (4): 824.
Protosialis australis Navas, 1927, Broteria, Zool. **24**: 28.

Tillyard described and figured this species from a single very damaged specimen. I have examined a further 9 specimens, 7 being females. Seven of the specimens are from Brisbane, not far from the type locality, Mt. Tambourine; the 8th is from Stanthorpe, Queensland; and the 9th is from Lane Cove River, near Sydney. This last specimen bears the collection label of R. J. Tillyard and is referred by him (1926) to a distinct but as yet undescribed species. There is difference neither in wing venation nor in male genitalia and the specimen cannot be separated from typical *australiensis*. It is considered therefore to be of that species, which probably will be found to range over most of the east coast zone of Australia. Navas (1927) based his description of *australis* on a specimen from Melbourne.

Female

Head brownish, darker on posterior border of occiput, except for 3 or 4 pale, raised, circular areas on either side of the midline, which itself is of a lighter colour than the rest of the occiput. Eyes relatively large, black. Antennae long and tapered, dark brown, almost black, with basal segment large and lighter in colour. Prothorax brownish, as wide as occiput, twice as wide as long, with irregular slightly darker areas. Meso- and metathorax reddish brown, wider than prothorax, upper surface strongly raised, with bulbous scutum. Legs light brown, similar in structure to those of *Sialis*, and with the expanded, bilobed 4th tarsal segment. Wings pale smoky brown. Fore wing with narrow

AUSTRALIAN MEGALOPTERA OR ALDER-FLIES



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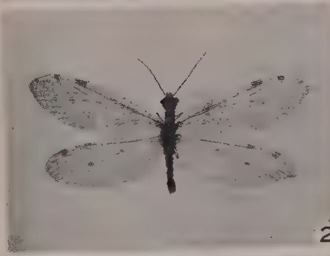

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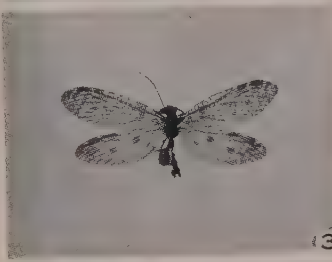

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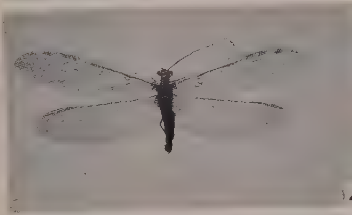

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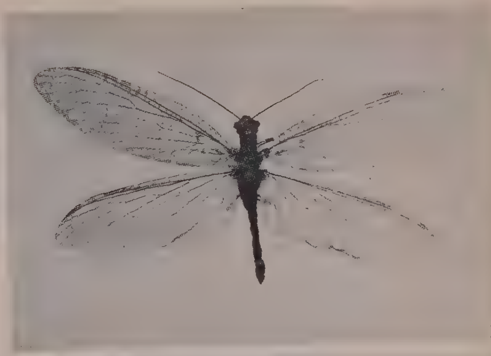

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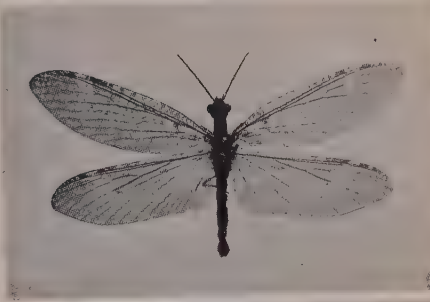

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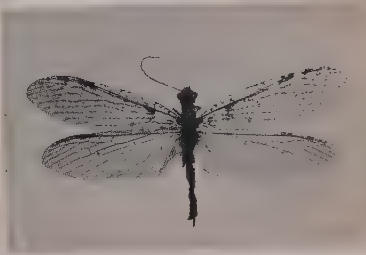

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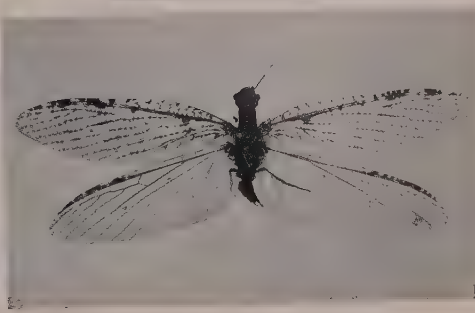

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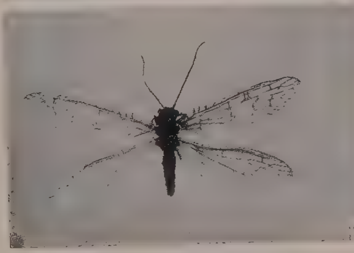

9

costal space, widened somewhat basally, with up to about 10 cross veins, of which only the 4 basal are distinct, the hind wing with 2 or 3 and sometimes traces of others. Abdomen almost black, genitalia reddish brown.

Male

Similar to the female but somewhat smaller (wing expanse up to 19 mm whereas that of the female reaches 27 mm), costal space more expanded and with the costal cross veins less well developed. Genital lobes with truncate apices, a small bulbous projection in the depression separating them.

Type: Holotype ♀ in Tillyard Collection, British Museum.

Type locality: Mt. Tambourine, south-eastern Queensland, 17.xii.1916 (W. H. Davidson).

Distribution.—The species is recorded also from Brisbane and Stanthorpe, Queensland, and from Lane Cove River, N.S.W. in the Division of Entomology Museum, C.S.I.R.O., Canberra, the Queensland Museum, and the University of Queensland; also from Melbourne (Navas).

Tillyard considers the type specimen as a female, with which I concur, though the costal margin in his figure of the fore wing is inaccurate and should show a slightly greater basad expansion of the costal area. I have examined 2 male specimens, one from Brisbane and the other from Lane Cove.

ACKNOWLEDGMENTS

The photographs are the work of Mr. D. Wilson, Division of Entomology, C.S.I.R.O., while the retouching of the prints and arrangement of the plate were done by Mr. L. A. Marshall, Division of Entomology, C.S.I.R.O. I am most grateful for their assistance.

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EXPLANATION OF PLATE 1

Fig. 1.—*Archichauliodes guttiferus guttiferus* (Walker), ♂, Cotter River, A.C.T. × ¾.

Fig. 2.—*Archichauliodes guttiferus polypastus*, subsp. nov., ♀, allotype, Lamington National Park, Queensland. × ¾.

Fig. 3.—*Archichauliodes guttiferus phaeoscius*, subsp. nov., ♂, holotype, Cairns district, Queensland. × ¾.

Fig. 4.—*Archichauliodes diversus* (Walker), ♂, Nelson, N.Z. × ¾.

Fig. 5.—*Austrochauliodes dubitatus* (Walker), ♀, Bunya Mountains, Queensland. × ¾.

Fig. 6.—*Austrochauliodes dubitatus* (Walker), ♂, Lamington National Park, Queensland. × ¾.

Fig. 7.—*Archichauliodes anagaurus*, sp. nov., ♂, holotype, Mt. Kosciusko, N.S.W. × ¾.

Fig. 8.—*Archichauliodes anagaurus*, sp. nov., ♀, allotype, Mt. Kosciusko, N.S.W. × ¾.

Fig. 9.—*Austrosialis australiensis* (Tillyard), ♀, Brisbane, Queensland. × 1½.

LIST OF SPECIES

Genus *Archichauliodes*
A. anagaurus, sp. nov. 136
A. guttiferus (Walker) 133
A. guttiferus guttiferus (Walker) .. 134
A. guttiferus phaeoscius, subsp. nov. 135
A. guttiferus polypastus, subsp. nov. 135

Genus *Austrochauliodes*
A. dubitatus (Walker) 137

Genus *Austrosialis*
A. australiensis (Tillyard) 140
A. ignicollis Tillyard 139

THE AUSTRALIAN MECOPTERA OR SCORPION-FLIES

By E. F. Riek[*]

[*Manuscript received September* 10, 1953]

Contents

Summary 143
Introduction 143
Systematics 144
    Key to Australian families of the Order Mecoptera 144
    Family Meropeidae 144
    Family Panorpidae 145
    Family Choristidae 146
    Family Bittacidae 155
Acknowledgments 166
References 166
List of species 168

Summary

This paper deals with the systematics of all known Australian Mecoptera. Two new species are described: *Austrobittacus anomalus* (*Austrobittacus* is a new genus) and *Harpobittacus phaeoscius*; and three new subspecies: *Harpobittacus australis rubripes, H. tillyardi albatus,* and *H. t. rubricatus.*

Introduction

This paper deals only with the systematics of the Recent species. In succeeding papers the biology of some of the species will be discussed. The number of known Australian Mecoptera has increased considerably since the appearance of Esben-Petersen's (1921) monograph of the Order. The 15 species belong to five families—Panorpidae, Choristidae, Nannochoristidae, Bittacidae, and Meropeidae. The Panorpidae and Meropeidae are represented respectively by the wingless *Apteropanorpa tasmanica* Carpenter of Tasmania and *Austromerope poultoni* Killington of Western Australia. The other three families are widespread. In the Choristidae there are a single species of *Taeniochorista* and two of *Chorista.* A species in the latter genus previously considered as a synonym is reinstated as a subspecies. The Nannochoristidae are represented by three well-defined species of *Nannochorista,* one of which is divisible into Tasmanian and mainland subspecies. In the Bittacidae there are a single species of the aberrant *Kalobittacus* and six of *Harpobittacus,* one species and two subspecies of the latter genus being described as new. The genus *Austrobittacus* is erected for a species resembling *Kalobittacus.*

The family Choristidae and to a less extent the family Nannochoristidae are characteristically Australian. The Nannochoristidae are found mainly in Tas-

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mania and south-eastern Australia, but species occur also in New Zealand and South America. The Choristidae have not been recorded outside Australia, where there are two Recent genera.

SYSTEMATICS

KEY TO AUSTRALIAN FAMILIES OF THE ORDER MECOPTERA

1. Each tarsus with 1 claw, and modified to raptorial use by folding down the terminal segment against the 4th........................Family Bittacidae
Each tarsus with 2 claws, tarsus normal in shape..........................2

2 (1). Wings with very dense and irregular venation; ocelli absent....Family Meropeidae
Wings when present long and slender and with open venation; ocelli present......3

3 (2). In the fore wing *CuA* does not fuse with the main stem of *M* (wings absent in *Apteropanorpa*)..................................Family Panorpidae
In the fore wing *CuA* coalesces with the main stem of *M* for a shorter or longer distance...4

4 (3). In the fore wing *CuA* only touches the main stem of *M*; *Rs* of 4 branches........ Family Choristidae
In the fore wing *CuA* and the main stem of *M* coalesce for a longer distance; *Rs* of 3 branches (R_{1+2}, R_3, R_4)....................Family Nannochoristidae

Family **MEROPEIDAE**

This small family is known only from North America and Australia. *Merope* is restricted to the eastern part of the United States while *Austromerope poultoni* Killington has been recorded only from Western Australia.

Genus AUSTROMEROPE Killington

Austromerope Killington, 1933, Ent. Mon. Mag. **69**: 2.

Genotype *Austromerope poultoni* Killington, 1933.

"Head closely appressed to the underside of the thorax, and thus only partly visible from above; rostrum short; eyes reniform, narrowly separated above; antennae short and similar in form to those of *Merope*. Prothorax as wide as the head, narrower than the rest of the body; transverse, but less so than in *Merope*; anteriorly rounded. Legs densely clothed with transverse rows of short setae; apex of tibiae with two spurs; claws with minute teeth at the base (in *Merope* the claws are simple). Anal forceps of male very long, the basal segment with a strong apical spine. The margins of both pairs of wings closely set with dot-like thickenings, from which arise short hairs. These marginal thickenings very closely resemble those seen in the Neuropterous family Hemerobiidae. The wings differ from those of *Merope* in the following respects. They are narrower, and thus relatively more elongate; the thickened lobe near the base of the inner margin of the forewing is rather less developed; in both the fore- and hindwings there is a more profuse branching of *R* and *M*, the first branch off from *Rs* showing five or six bifurcations, that from *M* two; cross-veins much more numerous; costal cross-veins longer and more or less parallel with the costal margin, several of these cross-veins in the middle of the costal area being forked. The venation of both *Merope* and *Austromerope* is somewhat unstable, but in general the characters given will undoubtedly hold true."

AUSTROMEROPE POULTONI Killington

Austromerope poultoni Killington, 1933, Ent. Mon. Mag. **69**: 2.

This species is known only from the male holotype.

Type: Holotype ♂ in the Hope Department, University Museum, Oxford.

Type locality: Near Perth, W.A., 31.vii.1914 (E. B. Poulton).

Family **PANORPIDAE**

This family is represented in the Australian fauna by the wingless *Apteropanorpa tasmanica* Carpenter, which occurs on the higher peaks of Tasmania. The family is essentially a Holarctic one, but is also present in India and the East Indies.

The Choristidae and Nannochoristidae of Tillyard are often considered subfamilies of the Panorpidae, but are here accorded family rank.

Genus APTEROPANORPA Carpenter

Apteropanorpa Carpenter, 1941, Pap. Roy. Soc. Tasm. **1940**: 51.

Genotype *Apteropanorpa tasmanica* Carpenter, 1941.

"Both sexes completely apterous, without indications of wing vestiges. Head large, much as in *Panorpa,* with a conspicuous rostrum, fully as large as that in *P. conigera* McL.; eyes small, only slightly protruding; ocelli absent; antennae elongate, with about 60 segments; clypeus broad, more remote from antennal insertions than in *Panorpa*; subgenal suture weak, subgenal processes very inconspicuous; labium long; mandibles toothed as in other Panorpids; maxillary palpi long, similar to those in *Panorpodes*; labial palpi small; thoracic nota contiguous, forming a heavy dorsal shield; 1st abdominal tergite fused with the metanotum; legs slender, typically panorpid, with smooth tarsal claws; abdomen very large and bulbous, with minute dorsal and ventral sclerites. *Female* abdomen: 9th abdominal sternite divided, forming two elongate plates, much as in *Panorpodes*; 10th abdominal sternite apparently absent (or very lightly sclerotized); 11th reduced to a small median plate; cerci long. There is apparently no internal skeleton (vulvar retractor apodeme) in the 9th abdominal segment. *Male* abdomen: Tergites 2-6 small; tergites 7 and 8 coalesced with their sternites, forming a ring around the abdomen; 7th and 8th abdominal segments very short; 9th and 10th essentially as in *Panorpa,* forming a bulb which is curved over the 7th and 8th segments. The styles (forceps) of the coxopodites of 9th segment are in the form of small, cylindrical processes directed inward and apparently attached to part of the 11th segment. The cerci absent or very minute."

APTEROPANORPA TASMANICA Carpenter

Apteropanorpa tasmanica Carpenter, 1941, Pap. Roy. Soc. Tasm. **1940**: 52.

Types: Holotype ♂ and allotype ♀ and 1 ♀ paratype in Museum of Comparative Zoology. Two ♀ paratypes in the Australian Museum.

Type locality: Holotype Mt. Mawson, allotype Mt. Wellington.

TASMANIA: Mt. Mawson and Mt. Wellington.

Family CHORISTIDAE

The family is restricted to Australia, where there are two genera.

Costal area of fore wing with only a basal cross vein. *Chorista* Klug
Costal area of fore wing with more than 1 cross vein. . . . . *Taeniochorista* Esben-Petersen

Genus CHORISTA Klug

Chorista Klug, 1836, Abh. Königl. Akad. Wiss.: 101.
Euphania Westwood, 1846, Trans. Ent. Soc. Lond. **4**: 188.

Genotype *Chorista australis* Klug, 1836.

Wings narrow, longer than the body, narrowed towards the rounded apex; fore wing about 3 times longer than broad. Costal area with a basal cross vein. *Sc* joins the costa before pterostigma. In both pairs of wings *CuA* and the main stem of *M* just touch each other or fuse for a short distance. In the fore wing 2*A* runs almost parallel to 1*A* for its whole length.

KEY TO SPECIES OF THE GENUS CHORISTA

1. Maxillary palps not greatly swollen (slightly so in male); 2 or 3 (rarely 1) cross veins from R_1 to costal margin. (Antennae with the basal 2 segments and portion of 3rd reddish brown; veins of wing without diffuse pigmentation) . . . . *C. ruficeps* (Newman)
Maxillary palps swollen; no cross veins from R_1 to costal margin between ending of *Sc* and pterostigma 2

2 (1). Antennae with basal 2 segments and portion of 3rd reddish brown, rest blackish; veins of wing with only a narrow band of diffuse pigment; ventral process from gonostylus of male about as long as broad . . . . . . *C. australis australis* Klug
Antennae with basal 7 segments and portion of 8th reddish brown, rest blackish brown; veins of wing with more diffuse pigmentation, particularly at origin of *M* from *R*; ventral process from gonostylus of male much broader than long . . . . *C. australis luteola* (Westwood)

The species of *Chorista* appear to be restricted to south-eastern Australia while the related *Taeniochorista* is found in Queensland and the northern part of coastal New South Wales. *Chorista ruficeps* occurs in both Victoria and New South Wales. *C. australis australis* has a distribution over most of New South Wales and Victoria but is not recorded from coastal New South Wales where *C. australis luteola* occurs.

CHORISTA AUSTRALIS Klug

Plate 1, Fig. 1

Chorista australis Klug, 1836, Abh. Königl. Akad. Wiss.: 101; Walker, 1853, List. Neur. Ins. Brit. Mus. **2**: 454; Tillyard, 1918, (in part) Proc. Linn. Soc. N.S.W. **43**: 395; Esben-Petersen, 1921, (in part) Coll. Selys. **5**: 98.

Head and rostrum yellowish brown. On the vertex a blackish area enclosing the ocelli or an isolated black area around each ocellus. Antennae slender, longer than the wings, blackish, the basal 2 segments and portion of the 3rd reddish brown. Maxillary palpi strongly swollen, particularly 3rd and 4th segments; inner surface of apical segment with numerous stout black spines; basal segment of labial palpi produced into a wide lateral flap. Thorax black, slightly lighter in colour ventrally. Abdomen black except for the terminalia, which are yellowish brown. Legs almost black except for the femora, which are yellowish brown except for the extreme base and a band at the apex. Wings with yellowish brown tinge, yellowish basally and with brown venation except for the basal ½ of *C* and *Sc* and the extreme bases of the other longitudinal veins. In the hind wing the whole basal ½ has yellowish venation. In the fore wing the veins are faintly shaded with brown but in the hind wing this is only noticeable at the apex. Pterostigma long, dark brown, very distinct. Cross veins not present from R_1 to anterior margin between costal ending of *Sc* and pterostigma.

Male terminalia.—Epiandrium not produced, only as long as the gonocoxite, broad, nearly quadrate, apical margin not produced into a spine; hypandrium keel-shaped, gradually narrowed towards the tip, with a deep wide cleft, the margin of this cleft being further excised near the apex of the hypandrium to give the appearance of 2 apical lobes. Aedeagus not produced beyond the folded stylus of the gonopods. Gonostylus with a forwardly directed basitubercle and the meditubercle developed as a ventral truncate process ending in a tuft of hairs, the structure being about as long as broad. Ventral valve of phallosome not strongly sclerotized or produced posteriorly.

Size

Length of fore wing 13.0-15.5 mm.

Type: Holotype ♀ in the Berlin Museum.

Type locality: New Holland.

Distribution.—Probably most of the south-eastern portion of Australia—widespread in Victoria and inland New South Wales. There is one doubtful record from the National Park, south-eastern Queensland.

This distinct species has been confused with its subspecies *luteola* (Westwood), which occurs on the coast of New South Wales. The latter differs in the pigmentation of the antennae and of the wings as well as in male terminalia. The species occurs commonly in the autumn, when large numbers can be seen on the vegetation, particularly grasses, bordering small streams. Specimens in some localities are preyed on by *Harpobittacus australis*, which has somewhat similar habits. In copulation the pair form a V, the abdomen of the female being straight and that of the male curved. During copulation there is an exchange of fluids between the mouths of the two, the mouth appendages showing constant movement.

CHORISTA AUSTRALIS LUTEOLA (Westwood)

Plate 1, Fig. 2

Euphania luteola Westwood, 1846, Trans. Ent. Soc. Lond. 4: 188; Walker, 1853, List. Neur. Ins. Brit. Mus. 2: 464.

Chorista australis Tillyard, 1918, (in part) Proc. Linn. Soc. N.S.W. 43: 395; Esben-Petersen, 1921, (in part) Coll. Selys. 5: 98; Crampton, 1931, Psyche, Camb., Mass. 38: 20.

Head and rostrum yellowish brown. Vertex drawn out into a rather high crown, very little black pigment around the ocelli, this being separated into 3 areas corresponding to the ocelli. Antennae slender, longer than the wings, blackish brown, the basal 7 segments and portion of the 8th yellowish brown, the basal 2 segments more deeply pigmented. Maxillary palps not greatly swollen except for the 2nd segment, and to some extent the 3rd; scattered black bristles over portions of all segments.

Thorax blackish, lighter in colour on the ventral side. Abdomen black except for the terminalia, which are yellowish brown. Legs blackish brown except for the femora, which are yellowish brown with a blackish apical band. Wings with a yellowish brown tinge, more yellowish towards the base. Venation of fore wing deep brown except for the bases of the longitudinal veins and for the basal ½ of *Sc* and most of *C*, which are yellowish. In the hind wing most of the basal ½ of the venation is yellowish. In the fore wing the veins are deeply shaded with brown while at the origin of *M* from *R* the membrane of the wing is shaded almost to the origin of *Rs* in some specimens, while in others it is more localized around the origin of *M*. In the hind wing the shading of the veins is only noticeable in the apical region. Pterostigma long, dark brown, very distinct. Cross veins not present from R_1 to anterior margin between costal ending of *Sc* and pterostigma. M_4 of fore wing arises close to the thyridium.

Male terminalia.—Epiandrium not produced, only slightly longer than the gonocoxite, broad, tapering somewhat to the truncate apex. Hypandrium keel-shaped, of almost parallel sides, with a deep wide cleft, the margin of this cleft being further excised near the apex of the hypandrium to give the appearance of 2 apical lobes on either side of the cleft, curved slightly towards one another. Aedeagus not produced beyond the folded stylus of the gonopods. Gonostylus with a forwardly directed basitubercle and with the ventral truncate meditubercle ending in a tuft of hairs, and very nearly as long as broad. Ventral valve of phallosome slightly produced posteriorly and with a few fine teeth towards the apex on the mesal side. The genitalia of this form have been figured by Crampton (1931) as *Chorista australis* Tillyard.

In the female the apical segments of the abdomen are reddish brown while the styles are almost black.

Size

Length of fore wing 12-15 mm.

Type: Holotype ♀ in the British Museum.

Type locality: The type is without locality data.

Distribution.—The subspecies is known only from the coastal areas of New South Wales.

This subspecies has been confused with typical *australis* Klug. As mentioned earlier it differs in pigmentation of antennae and wings as well as in the shape of the male terminalia. Esben-Petersen (1921) figured the wing of this form under *australis*.

CHORISTA RUFICEPS (Newman)

Panorpa ruficeps Newman, 1850, The Zoologist; Walker, 1853, List. Neur. Ins. Brit. Mus. 2: 464.

Chorista ruficeps Esben-Petersen, 1921, Coll. Selys. 5: 99.

Chorista victoriensis Issiki, 1931, Ann. Mag. Nat. Hist. (10) 7: 219.

Head and rostrum yellowish brown. Vertex drawn out into a rather high crown, very little black pigment around the ocelli, this being separated into 3 areas corresponding to the ocelli. Antennae slender, longer than the wings, blackish, the basal 2 segments and portion of the 3rd reddish brown. Maxillary palpi not swollen, rather long and slender. Few long bristles at the apex of each segment.

Thorax blackish, slightly lighter in colour ventrally. Abdomen black except for the terminalia, which are yellowish brown. Legs dark reddish brown, almost black, with joints black. Femora and trochanters reddish brown. Hind tibia with basal 2/5 covered with a dense bush of minute black hairs, especially on the posterior surface. Wings hyaline with a very slight yellowish brown tinge. Veins pale brown, not shaded, yellowish in basal area; pterostigma yellowish, opaque, indistinct, 2 or 3 cross veins (rarely only 1) from R_1 to anterior margin, between the costal ending of Sc and pterostigma. M_4 in fore wing originates very close to the thyridium.

Male terminalia.—Epiandrium not produced, a little shorter than the gonocoxite, broad, nearly quadrate, apical margin produced in the middle to a minute triangular process; a shallow depression just basad to the process; hypandrium keel-shaped, gradually narrowed towards the tip, with a deep narrow cleft, the margin of this cleft being further excised near the apex of the hypandrium to give the appearance of 2 apical lobes, the upper much longer than the lower. Aedeagus not produced beyond the folded stylus of the gonopods, but more or less on a level with them. Gonostyles short and stout, narrowing somewhat to the sharply truncate apex; basitubercle absent and antero-ventrally directed meditubercle rounded at the apex, not apposed to that of the other side and lacking the apical tuft of hairs. Ventral valve of phallosome strongly sclerotized, elongate, and produced posteriorly into 3 sharp spines.

Size

Length of fore wing 15-16 mm.

Type: Location of type not known.
Type locality: Australia.

Distribution.—New South Wales and Victoria.

Issiki (1931) described *victoriensis* from a single male specimen, the description of which falls within the range of variation of *ruficeps* (Newman). Variation in species of the genus *Chorista* is usual. In this species the number of cross veins between R_1 and the anterior margin is variable, as also is the coloration of the posterior abdominal segments. Issiki states that the penis of *victoriensis* extends beyond the folded gonostyles. I have not found this to be so but it may do so when in an exserted state of preservation.

Genus TAENIOCHORISTA Esben-Petersen

Taeniochorista Esben-Petersen, 1914, Ent. Medd. **2** (10): 129.

Genotype *Taeniochorista pallida* Esben-Petersen, 1914.

Wings not as long as the body; fore wing 2½ times longer than broad and with rounded apex. In the basal 2/3 of the costal area of fore wing 5-7 cross veins. *M* and *CuA* just touching or fused for a very short distance. In the fore wing *2A*, 1/3 from base, is curved towards *1A* or fuses with it for a short distance.

TAENIOCHORISTA PALLIDA Esben-Petersen

Plate 1, Fig. 3

Taeniochorista pallida Esben-Petersen, 1914, Ent. Medd. **2** (10): 129; Esben-Petersen, 1921, Coll. Selys. **5**: 100.

Head and rostrum yellowish brown; eyes black, ocelli large and prominent, each surrounded by a narrow brownish black circle more diffuse on the dorsal side. Dorsal (upper) side of anterior, unpaired ocellus with a pair of long, stout, black bristles. Antennae longer than wing, basal 2 segments and portion of 3rd yellowish brown, remaining segments a darker brown. Maxillary palps long and thin, 2nd segment with a distinct bulge on inner surface, 3rd segment inflated on inner side at both base and apex, 5th segment with the apical ½ devoid of long setae.

Thorax dark brown dorsally, lighter in colour ventrally. Abdomen dark brown above, yellowish brown ventrally and at apex. Legs light yellowish brown except for the basal 1/3 of the fore and middle tibiae, which are almost black; tarsi with apical row of black setae giving the appearance of a black band. Hind tibiae with the basal ½ somewhat swollen. Wings hyaline with a yellowish tinge; longitudinal veins and basal cross veins yellowish brown, remaining cross veins yellowish. Some specimens have a distinct transverse banding in the pigmentation of the apical ½ of the wing, this deeper pigmentation occurring in the areas between the cross veins but affecting the longitudinal veins.

Male terminalia.—Epiandrium not as long as the gonocoxites, relatively long and thin, with more or less parallel sides except for the rather sharply pointed apex. Hypandrium keel-shaped, tapering gradually towards the apex, with a deep, wide, apical cleft, the 2 primary lobes so formed being further subdivided on their inner apical sides into 3 smaller lobes, the middle being the shortest. Aedeagus not produced beyond the folded gonostyles. Gonostyles rather short, basitubercle absent, meditubercle situated on the ventral side at about ½ the length and directed antero-medially, long, truncate, somewhat longer than broad. Apex of gonostyle truncate, expanded somewhat on its ventral apical edge into a short, obtuse, blunt spine. Phallosome differing in shape from that found in *Chorista* but with the ventral valve elongate, sclerotized, but lacking any teeth.

Female similar to the male except that the maxillary palps are little if at all swollen.

Size

Length of fore wing 15-17 mm.

Type: Holotype ♂ in Esben-Petersen collection.
Type locality: Brisbane, Queensland, 11.v.1912 (H. Hacker).

Distribution.—Coastal portions of south-eastern Queensland and coastal New South Wales.

The slight banding of the wings is quite variable in a series from any given locality but other characters are more stable.

Family NANNOCHORISTIDAE

Costal area of usual breadth. Two cross veins between C and Sc in the fore wing, one in the hind wing. Sc joins R or C in the fore wing at a more or less wide distance from pterostigma; in the hind wing Sc joins C much before pterostigma. R_1, R_{2+3}, R_4, R_5, M_1, M_2, M_3, and M_4 are present in both pairs of wings. Both in fore and hind wing CuA and the main stem of M coalesce for a rather long distance. In the hind wing CuP and $1A$ only touch each other at a point. $1A$, $2A$, and $3A$ present in both fore and hind wing. Rostrum rather short and strongly pointed towards apex. Claws serrate basally. In the male the abdomen is short; all the segments except the terminal ones are narrow and transverse.

The family, represented by the two genera *Nannochorista* Tillyard and *Choristella* Tillyard, is known from Australia and Tasmania, New Zealand, and South America (*N. neotropica* Navas, 1928 from Chile and *N. edwardsi* Kimmins, 1929 from Argentine).

The New Zealand genus *Choristella* Tillyard can be separated from *Nannochorista* on wing venation:

Area between R_4 and R_5 divided by a cross vein into 2 cells........*Nannochorista* Tillyard
Normally, area between R_4 and R_5 not divided by a cross vein into 2 cells.............
Choristella Tillyard

KEY TO AUSTRALIAN SPECIES OF THE GENUS NANNOCHORISTA

1. Sc terminating in C..................................*N. holostigma* Tillyard
Sc terminating in R_1..2
2 (1). Head black; wings heavily pigmented................*N. maculipennis* Tillyard
Head not completely black; wings with very little pigment........*N. dipteroides dipteroides* Tillyard and *dipteroides eboraca* Tillyard

Genus NANNOCHORISTA Tillyard

Nannochorista Tillyard, 1917, Proc. Linn. Soc. N.S.W. **42**: 292.

Genotype *Nannochorista dipteroides* Tillyard, 1917.

Hind wing somewhat shorter than the fore wing. In the fore wing *Sc* terminates in *C* or in R_1; between *C* and *Sc* 2 cross veins. In the hind wing *Sc* is very short and terminates in *C*. One cross vein between *Sc* and *C*, and 1 between *R* and *C*. The area between R_4 and R_5 in both pairs of wings divided by a cross vein into 2 cells.

NANNOCHORISTA DIPTEROIDES DIPTEROIDES Tillyard

Nannochorista dipteroides Tillyard, 1917, Proc. Linn. Soc. N.S.W. **42**: 293; Esben-Petersen, 1921, Coll. Selys. **5**: 102.

Male

Head medium brown, eyes very dark brown, vertex and ocelli black. Antennae: Scape, pedicel, and base of 3rd segment brownish, rest black. Mouthparts brownish. Thorax black, a tinge of reddish brown near wing bases. Legs pale, semitransparent brownish, slightly darkened distally on each segment, tarsi darker. Abdomen: Segments 1-8 black, with a slight tinge of reddish brown at extreme base; all segments furnished with short pale hairs, segments 9-10 and gonopods rich brown, with hairs of same colour. Wings almost clear, diffuse pigmentation on a few of the cross veins. *Sc* of fore wing terminating in R_1. Gonopods over ½ as long again as broad. Gonostyle, in dorsal aspect, rather long and thin, over twice as long as broad, with the inner margin straight except at base, row of 12-15 teeth usually on inner margin, rather large in size and fairly evenly spaced except at apex, 2 apical ones enlarged, well separated.

Female

Head and thorax as in male except that the labrum and epipharynx are slightly longer. Abdomen shining black. First segment of the flagellum of the antenna relatively long, though not as long as in the male.

Size

Length of fore wing 6-8 mm.

Types: Holotype ♂, allotype ♀, and paratypes in Tillyard collection (British Museum). Paratypes in Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Hobart, on vegetation beside an overflow of the artificial channel that runs between Huon Road and Strickland Avenue.

TASMANIA: Hobart, Oct.-Nov. 1916 (G. H. Hardy and C. E. Cole); Mt. Wellington, Jan. 1917; Ben Lomond, 15.xii.1919; Dee Bridge, 7.ii.1933 (R. J. Tillyard); North Esk, 24.i.1933 (R. J. Tillyard).

There is considerable variation in the amount of pigmentation of the wing, some specimens approaching that typical of *holostigma* Tillyard, but the structure of *Sc* is diagnostic and separates the 2 species.

NANNOCHORISTA DIPTEROIDES EBORACA Tillyard

Nannochorista eboraca Tillyard, 1917, Proc. Linn. Soc. N.S.W. **42**: 295; Esben-Petersen, 1921, Coll. Selys. **5**: 104.

Head reddish brown, vertex and ocelli shining black. Antennae: Scape and pedicel reddish brown, rest black, 3rd segment long. Eyes black, mouth-parts blackish. Thorax dark shining brown. Legs very slender, semitransparent pale brownish, tarsi somewhat darker. Wings rather elongated, slightly clouded. Abdomen very dark shining brown. Gonopods over ½ as long again as broad. Gonostyle, in dorsal aspect, long and thin, 3 times as long as broad, with the inner margin straight except at base, row of 15-18 teeth, more crowded towards the base, apical tooth and next enlarged, well separated. First segment of the flagellum of the antenna of male very long, that of the female relatively long.

Size

Length of fore wing 7-7.5 mm.

Type: Holotype ♀ in Tillyard collection (British Museum).

Type locality: Ebor scrub, N.S.W.

NEW SOUTH WALES: Ebor scrub, 5000 ft, 11.i.1916 (A. J. Turner); Blundells, near Canberra, 10.x.1930 (W. K. Hughes) and 22.x.1938 (A. L. Tonnoir); Kosciusko, 17.xi.1938 (A. L. Tonnoir); Alpine Creek, 12.xi.1938 (A. L. Tonnoir).

The subspecies was described originally from a single female. Tillyard considered that it could be distinguished at once from *N. dipteroides* by the form of the cerci in the female. Tillyard's figures of the cerci of the Australian species, however, are erroneous, their differences depending on their state of preservation. Many specimens shrink considerably on drying. The form *eboraca* Tillyard is best considered as a subspecies of *dipteroides* Tillyard, being its mainland representative, and differing *inter alia* in the shape of the male terminalia.

There are 7 male specimens in the Division of Entomology Museum, C.S.I.R.O., Canberra, from the additional localities listed above on which the differences in the male terminalia are based.

NANNOCHORISTA HOLOSTIGMA Tillyard

Plate 1, Figs. 4, 5

Nannochorista holostigma Tillyard, 1917, Proc. Linn. Soc. N.S.W. **42**: 294; Esben-Petersen, 1921, Coll. Selys. **5**: 103.

Closely resembles *N. dipteroides*, from which, however, it may be distinguished at once as follows: In fore wing Sc terminates in C, not in R_1, and the pterostigma is completely closed proximally by a small cross vein descending from Sc to R_1. Wings slightly broader and generally somewhat less hyaline than in *dipteroides*; most of the cross veins in the fore wing usually distinctly clouded. Legs with a black spot on each trochanter, a black blotch distally on each femur. Segments 9-10 and gonopods of male rich red-brown. Gonopods ½ as long again as broad. Gonostyle, in dorsal aspect, rather long, slightly more than twice as long as broad, with inner margin straight except at base, row of 15-18 teeth more crowded towards the base, apical tooth and next enlarged, rather close together. First segment of the flagellum of the antenna of the male greatly lengthened, that of the female relatively short.

Size

Length of fore wing 6-8.5 mm.

Types: ♂, ♀, and paratypes in Tillyard collection (British Museum). Paratypes in Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Lakes Lilla and Dove, Cradle Mountain, Tas.

TASMANIA: Shores of Lakes Lilla and Dove, Cradle Mountain; Lake St. Clair, 25.i.1949 (E. F. Riek); Lake Fenton, 21.i.1949 (E. F. Riek).

This species is distinguished from all other Australian species by the structure of *Sc*, which terminates in *C* and not in R_1 as is usual.

NANNOCHORISTA MACULIPENNIS Tillyard

Nannochorista maculipennis Tillyard, 1917, Proc. Linn. Soc. N.S.W. **42**: 294; Esben-Petersen, 1921, Coll. Selys. **5**: 103; Evans, 1942, Trans. Roy. Soc. S. Aust. **66**: 218.

This very distinct species differs from *dipteroides* as follows: Head entirely black, antennae 22-segmented, black, 3rd segment not much elongated. Thorax and abdomen: Abdomen segments 1-8 jet black, 9, 10, and gonopods dark brown, large, blunter than in *dipteroides*, somewhat hairy. The gonostyle differs markedly from the other Australian species; basitubercle strongly developed, with a slight anterior curvature; meditubercle also strongly developed, about the middle of the mesial surface; a number of other small spines along this inner surface and a large apical one but no penultimate one enlarged (description of gonostyle from the figure by Evans (1942)). Wings distinctly shorter and more rounded at apices than in the other species; fore wing heavily clouded with greyish black upon all the cross veins and junctions of the veins. Hind wings with cross veins near middle of wing lightly clouded.

Size

Length of fore wing 5.5-6 mm.

Type: Holotype ♂ in Tillyard collection (British Museum).

Type locality: Crater Lake Creek, Cradle Mountain, Tas.

TASMANIA: Wilmot (Carter and Lea); Mt. Wellington, near Hobart, Feb. 1941 (J. W. Evans).

The species was described originally from a unique male specimen but Evans (1942) stated that it was very common on Mt. Wellington in February 1941. There is a single female specimen from Wilmot in the Division of Entomology Museum, C.S.I.R.O., Canberra. Evans has given a full account of the morphology of both sexes, which can be distinguished by the black head and by the gonostyle of the male.

The female specimen from Wilmot in the Division of Entomology Museum, C.S.I.R.O., Canberra, is abnormal in that in addition to the usual 3 ocelli there is another pair, lying behind and somewhat laterad of them. In size the extra ocelli are smaller and are not raised above the general surface to the extent of the normal ones. Further, at the posterior margin of each arises a long, stout, black bristle.

Family BITTACIDAE

This tipuliform family is recognized easily by the slenderness in all parts and especially by the modified tarsi, in which the terminal segment bears only 1 claw and may be reflexed against the 4th. The family is found in all parts of the world except the northern parts of the Holarctic region.

Three genera are represented in the Australian fauna. *Harpobittacus* is widespread though restricted to Australia. *Kalobittacus* was originally described from Mexico. *Austrobittacus* is erected for a small Queensland species somewhat resembling a *Kalobittacus*.

Key to Australian Genera of the Family Bittacidae

1. In the fore wing 1*A* and 2*A* connected by a single cross vein; in the hind wing *CuP* and 1*A* fused for their whole length........................*Kalobittacus*

In the fore wing 1*A* and 2*A* connected by 2 cross veins; in the hind wing *CuP* and 1*A* free for parts of their length.................................2

2 (1). Basal segment of hind tarsus considerably longer than 4th; in hind wing the apical cross vein lies between 2*A* and the fused *CuP* and 1*A*, *CuP* and 1*A* separating after the separation of *M* and *CuA*................*Austrobittacus*

Basal and 4th segments of the hind tarsus subequal; in hind wing the apical cross vein lies between 2*A* and the free apical portion of 1*A*, *CuP* and 1*A* separating before the separation of *M* and *CuA*......................*Harpobittacus*

Genus KALOBITTACUS Esben-Petersen

Kalobittacus Esben-Petersen, 1914, Ent. Medd. **2** (10): 131.

Genotype *Kalobittacus bimaculatus* Esben-Petersen, 1914.

Differs from *Bittacus* in the marked coalescence of *CuP* and 1*A* in the hind wing and in having 1*A* very short in the fore wing. In the fore wing 1*A* is hardly ½ *CuP*; 2*A* is also short, 2/3 the length of 1*A*, and connected to it by a single cross vein; 3*A* minute. In the hind wing 1*A* coalesces with *CuP* for all its length and joins the hind margin a little beyond the separation of *M* and *CuA*; 2*A* short, 1/3 the length of 1*A*; 3*A* minute. Eyes almost as far apart in front as the width of the rostrum at its base. Basal segment of the hind tarsus longer than the 2nd and 3rd which are equal, combined; 4th 1/2-2/3 of 1st; 5th a little longer than 3rd.

The genus was known only from the holotype of *bimaculatus* from Mexico but *Bittacus microcercus* Gerstaecker, 1885, obviously belongs to the genus.

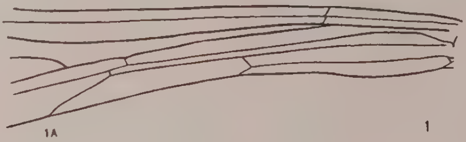
Kalobittacus microcercus (Gerstaecker)

Figs. 1, 2

Bittacus microcercus Gerstaecker, 1885, Mitt. naturw. Ver. Greifswald, **16**: 119; Esben-Petersen, 1921, Coll. Selys. **5**: 127.

General colour reddish brown with darker head; face and rostrum dark reddish brown; maxillary palpi brown; vertex reddish brown; ocelli with blackish brown markings extending laterally to the eyes; antenna dark brown; thorax and abdomen pale reddish brown; legs reddish brown, darkened at joints; wings with yellowish brown tinge, especially the pterostigma and the anterior border from the pterostigma to the apex.

Epiandrial lobes of male, seen from above, pointed, with slightly inturned apex bearing small black teeth on the inner surface; in lateral view triangular, tapering rapidly to the apex. Hind margin of the 9th abdominal tergite emarginate at meson. Between *Rs* and the pterostigma there are normally 2 cross veins in each wing.



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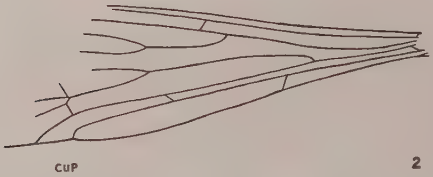

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Figs. 1, 2.—*Kalobittacus microcercus* (Gerstaecker). Fig. 1.—Base of fore wing. × 5¼. Fig. 2.—Base of hind wing. × 2⅝.

Fore wing with 1*A* slightly less than ½ *CuP*, reaching the wing margin just before or after the separation of *M* and *CuA*; 2*A* slightly over ½ 1*A* and connected to it by a single cross vein; 3*A* minute, almost transverse, without distinct cross vein to 2*A*; a fine, minute jugal about as long as 3*A*. Hind wing with *CuP* and 1*A* fusing near the base and not separating till after the separation of *M* and *CuA*, and then with the apical portion of 1*A* almost transverse (in some specimens this apical portion of 1*A* disappears); 2*A* very short, less than 1/3 1*A*, with a single cross vein to 1*A*; 3*A* very short, almost ½ 2*A*, with a cross vein to 2*A* from its apex at the wing margin; a minute transverse jugal at the base.

Size

Length of body, ♂ 15 mm, ♀ 14 mm; length of fore wing, ♂ 16.5 mm, ♀ 15 mm.

Type: Holotype ♂ in Museum Greifswald, Germany.

Type locality: Peak Downs, Queensland.

QUEENSLAND: Olsen's Caves, 13 miles N. of Rockhampton, 25.iii.1950 (I. F. B. Common). The National Museum, Melbourne, has a series of specimens, including both sexes, from an unspecified locality in Queensland.

Genus AUSTROBITTACUS, gen. nov.

Genotype *Austrobittacus anomalus*, sp. nov.

Differs only slightly from *Bittacus*, but the hind wing has a shorter 1*A* and more fusion between *CuP* and 1*A*, with these veins separating after the separation of *M* and *CuA*. The apical cross vein from 2*A* touches the fused *CuP* and 1*A* and not the free apical portion of 1*A*. Eyes wide apart below the antennae. Basal segment of hind tarsus longer than 4th.

AUSTROBITTACUS ANOMALUS, sp. nov.

Figs. 3, 4; Plate 1, Fig. 6

General colour reddish brown, with darker head; face and rostrum dark reddish brown; maxillary palpi brown; vertex widely reddish brown; ocelli with reddish brown markings not extending to the eyes; antennae dark brown; thorax pale reddish brown; abdomen pale reddish brown darkened from apex of 6th segment to terminalia, especially in male; legs pale reddish brown, darkened at joints; wings with yellowish brown tinge, especially the pterostigma and the anterior border from the pterostigma to the apex.

Epiandrial lobes of male, seen from above, very long and narrow, almost parallel with incurved apex bearing a few black teeth on the inner surface. In lateral view very long and thin, with subparallel sides and rounded apex. Hind margin of 9th abdominal tergite slightly emarginate at meson.

Fore wing with 1*A* about ½ the length of *CuP*, reaching the wing margin somewhat after the separation of *M* and *CuA*; 2*A* about 2/3 of 1*A* and connected to it by 2 cross veins, the longer almost at the apex of 2*A*; 3*A* minute, almost transverse, with a cross vein to 2*A* near its base; a very minute jugal about 2/3 the length of 3*A*. Hind wing with *CuP* and 1*A* fusing near base and not separating till slightly after the separation of *M* and *CuA*, and then with 1*A* passing very obliquely to the wing margin so that it is slightly more than ½ *CuP*; 2*A* somewhat more than ½ 1*A* and with 2 cross veins to it; 3*A* very short, about 1/3 of 2*A*, parallel to 2*A* and with a cross vein to it from near its apex; a minute transverse jugal at the base.

Size

Length of body, ♂ 15 mm, ♀ 14 mm; length of fore wing, ♂ 15 mm, ♀ 15 mm.

Types: Holotype ♂, allotype ♀, and paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Rockhampton, Queensland.

QUEENSLAND: Rockhampton, 23.iii.1950 (I. F. B. Common); Olsen's Caves, 13 miles N. of Rockhampton, 25.iii.1950 (I. F. B. Common).

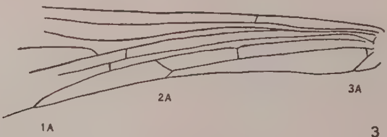
The species has a most distinctive venation. It can also be recognized on the male terminalia, the colour of the abdomen, and the vertex of the head. Although the venation differs rather markedly from that of *Kalobittacus* this species is of a rather similar size and build to *K. microcercus*.

Genus HARPOBITTACUS Gerstaecker

Harpobittacus Gerstaecker, 1885, Mitt. naturw. Ver. Greifswald **16: 119.**

Genotype *Bittacus australis* Klug, 1836.

Abdomen stout. Subgenital plate in the female very short. Hind femora strong and thick. First segment of hind tarsi of the same length as 4th, in the male a little longer. Wings long and narrow; hind border near to the base conspicuously curved inwards. As a rule 1*A* joins the hind margin opposite *Fm*. 2*A* scarcely ½ as long as 1*A*. Pterostigma very distinct and well marked.



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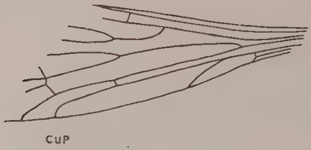

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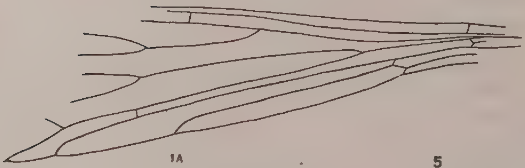

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Figs. 3, 4.—*Austrobittacus anomalus*, sp. nov. Fig. 3.—Base of fore wing. × 5¼. Fig. 4.—Base of hind wing. × 2⅝. Fig. 5.—*Harpobittacus nigriceps* (Selys). Base of hind wing. × 2⅝.

The genus apparently is restricted to Australia and Tasmania. The species fall naturally into 2 groups. In one group (*australis, tillyardi*, and *similis*) *Av* (the apical cross vein between *CuP* and 1*A*) is present, while in the other group (*nigriceps, scheibeli*, and *phaeoscius*) *Av* is absent. Species of the 2 groups occur together. For example, *nigriceps* and *australis* occur in Victoria while *scheibeli* and *tillyardi* have been collected at Brisbane, Queensland.

KEY TO SPECIES OF THE GENUS HARPOBITTACUS

1. Apical cross vein between *CuP* and 1*A* absent 2
   Apical cross vein between *CuP* and 1*A* present 3

2 (1). Head completely black; abdomen completely black . . . . *H. nigriceps* (Selys)
   Head completely black; abdomen reddish brown except for apical segments . . . . . . *H. phaeoscius*, sp. nov.
   Head with lower portion of face and basal portion of rostrum reddish brown; abdomen reddish brown except for apical segments . . . . *H. scheibeli* Esben-Petersen

3 (1). Abdominal segments 6 and 7 of male; 5, 6, and 7 of female completely black above 4

Abdominal segments 7 of male, 6 and 7 of female completely black above (fore and middle tibiae dark reddish brown except at apices; 9th abdominal segment of male with a strong median triangular backward projection on dorsal side, lateral projection short and stout, truncately rounded) . . . . *H. tillyardi tillyardi* Esben-Petersen

No abdominal segments dark above in male, none completely dark in female but 6 and 7 almost so (fore tibia dark reddish brown, middle tibia black or blackish; 9th abdominal segment of male with a strong median triangular backward projection on the dorsal side, lateral projection short, rounded at apex) . . . . *H. tillyardi rubricatus,* subsp. nov.

4 (3). Ninth abdominal segment of male with poorly developed backward projection on dorsal side, lateral projection long and thin, curved upwards, with a well-developed medianly directed tooth on the inner side; fore wing generally exceeding 20 mm 5

Ninth abdominal segment of male without a backward projection, lateral projection clubbed at apex, with a large posteriorly directed finger-like process developed from a flange on the inner side; fore wing generally not exceeding 19 mm (fore and middle tibiae black) . . . . *H. similis* Esben-Petersen

5 (4). Tibiae of fore and middle legs black . . . . *H. australis australis* (Klug)

Tibiae of fore and middle legs dark reddish brown except at apices . . . . *H. australis rubripes,* subsp. nov.

HARPOBITTACUS AUSTRALIS AUSTRALIS (Klug)

Plate 2, Figs. 1, 2

Bittacus australis Klug, 1836, Abh. Königl. Akad. Wiss.: 100; Walker, 1853, List. Neur. Ins. Brit. Mus. **2**: 467; Froggatt, 1902, Proc. Linn. Soc. N.S.W. **27**: 359.

Harpobittacus australis Gerstaecker, 1885, Mitt. naturw. Ver. Greifswald **16**: 119; Esben-Petersen, 1921, Coll. Selys. **5**: 156.

Male

Head reddish brown, vertex black, apical 2/3 of rostrum black, palps and antennae black. Thorax reddish brown except for dorsal surface of prothorax and anterior portion of mesothorax. Abdomen reddish brown basally, segments 6 and 7 completely black, remaining segments, including terminalia, reddish brown. Narrow apical band to segments 2-5 black.

Epiandrial lobes of male, seen from above, long and narrow with slightly incurved apex. In lateral view rather rectangular with the upper margin somewhat emarginate and the tip slightly rounded. The upper apical margin has short, stout, black spines on the inner surface. From the middle of the lower margin mesially is developed a long, stout, bluntly pointed spine-like structure directed more or less medially. Hind margin of the 9th segment on its dorsal side produced into a small, triangular, backwardly projecting spine.

Fore and middle legs blackish except for basal 1/3 of femora. Hind legs reddish brown, apex of femora and base and apex of tibiae black, tarsi black.

Wings light smoky brown, yellowish at base. Pterostigma very distinct, reddish brown. Two cross veins from pterostigma to *Rs*. No apical cross vein in the costal area. Subcostal cross vein in fore wing ½ way between origin of *Rs* and fork of *Rs*, in hind wing nearer to origin of *Rs*. Forking of *Rs* before the fork of *M*. Cubital cross vein present. Apical cross vein present between *CuP* and 1*A*.

Female

Similar to male except for abdominal coloration, segment 5, in addition to 6 and 7, being completely black, as too is the basal portion of 8.

Size

Varies considerably. Length of body, ♂ 19.5-26 mm, ♀ 18-23 mm; length of fore wing, ♂ 20.5-26 mm, ♀ 20.5-25.5 mm. Specimens collected late in the season are generally larger than those which are first to emerge.

Type: Holotype ♀. Location not known.

Type locality: New Holland.

Distribution.—Southern New South Wales, Victoria, Tasmania, and South Australia.

This widespread species, of which several hundred specimens were examined, is divisible into 2 subspecies. The typical form ranges from southern New South Wales through Victoria to South Australia and Tasmania. The northern form, which differs only in the coloration of the fore and middle tibiae (in which character it approaches *tillyardi*), is known from northern New South Wales and southern Queensland.

Currie (1932) has outlined the life history of this species under the name *H. tillyardi* E.-P.

HARPOBITTACUS AUSTRALIS RUBRIPES, subsp. nov.

Male

Similar to *australis autralis* except for the coloration of the fore and middle tibiae, which are reddish brown except narrowly at the apices.

Female

Similar to the male except for abdominal coloration, segment 5, as well as 6 and 7, being completely black.

Size

Length of body, ♂ 22-24 mm, ♀ 20 mm; length of fore wing, ♂ 22-23.5 mm, ♀ 23 mm.

Types: Holotype ♂, allotype ♀, and 11 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra. A further 7 paratypes in the Macleay Museum, Sydney.

Type locality: Barrington Tops, N.S.W., 7.iv.1949 (E. F. Riek).

NEW SOUTH WALES: Barrington Tops, 7.iv.1949 and Jan. 1925. QUEENSLAND: Brisbane, Sept. 1920 (R. Illidge); Stanthorpe, 11.x.1916.

Thirteen specimens were examined.

HARPOBITTACUS TILLYARDI RUBRICATUS, subsp. nov.

Plate 2, Figs. 3, 4

Male

Differing from *tillyardi tillyardi* in colouring of fore and middle legs and of abdomen, and in genitalia. Fore tibia dark reddish brown except for black apex, middle tibia darker, black or blackish. Abdomen above without any segment black though the 7th is dark laterally.

Epiandrial lobes relatively short, seen from above with only a slight inward curvature at the apex. In lateral view with upper and lower margins almost straight, slightly emarginate, apex rounded, rather pointedly. The upper apical margin, on its inner side, with a dense tuft of rather stout black spines on a raised flange-like projection which curves round to join the lower margin, so that when viewed from behind it gives the appearance of a hollow cone with spines on the upper ½ of its circumference. Viewed from above one sees a curved line of short, stout spines. Hind margin of the 9th segment on its dorsal side is produced backwards into an obtuse spine.

Female

Similar to the male except for abdominal coloration, segments 6 and 7 almost black but some reddish hues at meson, 5 dark laterally.

Size

Length of body, ♂ 18-22 mm, ♀ 16-20 mm; length of fore wing, ♂ 18-21 mm, ♀ 18-21 mm.

Types: Holotype ♂, allotype ♀, and 35 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Trangie, N.S.W., 20.x.1949 (E. F. Riek).

NEW SOUTH WALES (inland): Trangie, 40 miles W. of Bourke, 28.x.1949 (E. F. Riek); Bourke, 27.x.1949 (E. F. Riek); 35 miles NW. of Nyngan, 21.x.1949 (E. F. Riek); 65 miles NW. of Nyngan, 21.x.1949 (E. F. Riek).

The subspecies has distinctive abdominal coloration.

HARPOBITTACUS TILLYARDI TILLYARDI Esben-Petersen

Plate 2, Fig. 5

Harpobittacus tillyardi Esben-Petersen, 1915, Ent. Medd. **10**: 240; Esben-Petersen, 1921, Coll. Selys. **5**: 157.

Harpobittacus nigratus Navas, 1932*a*, Broteria **1**: 72; Navas, 1932*b*, Boll. Mus. Zool. Torino **42** (3): 27.

Male

Head reddish brown, vertex black; apical 2/3 of rostrum black, palps and antennae black. Thorax reddish brown except for the dorsum of the prothorax and the front ½ of the mesothorax, which are black. Abdomen reddish brown, the hind border of segments 2-6 narrowly blackish, 7th completely black above, remaining segments and genitalia reddish brown.

Epiandrial lobes of male relatively short and stout; seen from above they show only slight inward curvature at the apex. In lateral view both upper and lower margins emarginate, the upper one noticeably so, apex rounded. The upper apical margin, on its inner side, with numerous short stout black spines which continue, in an oblique line, towards the middle, on a raised flange-like projection which curves round to join the lower margin, so that when viewed from behind it gives the appearance of a hollow cone with spines on the upper ½ of its circumference. Viewed from above one has the impression of a short, stout, medially directed spine. The hind border of the 9th segment on its dorsal side is produced backwards into a long, triangular, projecting spine.

Legs reddish brown, apical ½ of fore and middle femora and apex of hind femora black; base of tibiae with a narrow, and apex with a broad, black band; fore tibiae rather dark brown; tarsi blackish.

Wings pale smoky brown, distinctly yellowish at base. Pterostigma reddish brown, relatively small, and with 2 cross veins connecting it to *Rs*. No apical cross veins in the costal area. Subcostal cross vein of fore wing about ½ way between the origin of *Rs* and the forking of *Rs;* in the hind wing at, very near, or sometimes even slightly before, the origin of *Rs*. Fork of *Rs* occurs before the fork of *M*. Cubital cross vein slightly before forking of *M*. Apical cross vein between *CuP* and 1*A* present.

Female

Similar to male but the hind borders of segments 2-5 are narrowly blackish above, segments 6 and 7 and basal part of 8 are black, remainder reddish brown.

Size

Length of body, ♂ 22-25 mm, ♀ 19-20 mm; length of fore wing, ♂ 21-24 mm, ♀ 21.5-24 mm.

Type: ♂ in Coll. Selys.

Type locality: New Holland. The type locality of *nigratus* is Sydney.

Distribution.—This species is widespread in the coastal zone of New South Wales and southern Queensland, being recorded from Brisbane, Stradbroke I., Woodford, and Noosa in Queensland, and from Sydney, Narrabeen, and Dorrigo in New South Wales.

Thirty-seven specimens were examined.

Harpobittacus tillyardi albatus, subsp. nov.

There is a distinct subspecies of *tillyardi* in the northern part of its range. It occurs at Rockhampton and surrounding areas and there is one doubtful record from Brisbane. The subspecies differs mainly in the genitalia of the male, but in general specimens are smaller and of paler body and wing coloration than the typical form.

In the male the spine from the 9th segment is smaller and the flange on the inner side is produced strongly and also more ventrally so that when viewed from behind one has more the impression of ½ a hollow cone with spines along the diameter and a little of the circumference. In lateral view the appendage tapers gradually to a rounded apex, at the same time curving slightly upwards.

Size

Length of body, ♂ 22 mm, ♀ 21 mm; length of fore wing, ♂ 22 mm, ♀ 23 mm.

Type: Holotype ♂ and allotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra. Three paratype ♂ ♂ in Macleay Museum, Sydney.

Type locality: Rockhampton, Queensland.

QUEENSLAND: Rockhampton; Eidsvold; (?) Brisbane.

Seven specimens were examined.

HARPOBITTACUS SIMILIS Esben-Petersen

Harpobittacus similis Esben-Petersen, 1935, Vidensk. Medd. Dansk. Naturh. Foren Kbh. **99**: 2.

Harpobittacus australis Weele, 1907, Die Fauna Sud-west Australiens 1: 225; Esben-Petersen, 1921 (in part), Coll. Selys. **5**: 156.

Male

Head black except for lower part of face and basal 1/3 of rostrum. Palps and antennae black. Thorax reddish brown on the under side, black dorsally except the meso- and metascutellum, which are reddish brown. Abdomen with the basal segments reddish brown with narrow black apices, segments 6 and 7 completely black, remaining segments reddish brown. Epiandrial lobes of male rather long and thin, slightly incurved, in lateral view almost rectangular, bearing rather long stout bristles on their inner side in the apical portion; with a strong postero-mesially directed blunt tooth arising from about the middle of the inner surface. Ninth abdominal segment without a backwardly directed spine.

Fore and middle legs blackish except for the basal 1/3 of the femora. Hind legs reddish brown, apex of femora, base and apex of tibiae, and tarsi black.

Wings pale smoky brown, pterostigma reddish brown, distinct bases of wings yellowish tinged. No apical cross vein in the costal area. Subcostal cross vein in the fore wing a little beyond origin of *Rs*, in the hind wing the cross vein is placed at the origin of *Rs* or a little before. Forking of *Rs* before fork of *M*. Cubital cross vein present. Apical cross vein between *CuP* and 1*A* present.

Female

Similar to male except that abdominal segments 5, 6, and 7 are all black.

Size

Length of body, ♂ 18.5-21 mm, ♀ 17-18 mm; length of fore wing, ♂ 17.5-19 mm, ♀ 18.5-19 mm.

Types: ♂ and ♀ in Esben-Petersen collection.

Type locality: Western Australia.

WESTERN AUSTRALIA: Perth; Yanchep; South Perth; Mogamber; Margaret River; Kalamunda; Cranmore Park; Mundaring; Guildford; Hovea; Cannington.

A series of 58 specimens was examined. This species is most similar to *australis australis,* differing from it only in its somewhat smaller size and in the genitalia of the male. I am unable to separate the females of the 2 species except on size, so it may be necessary to consider *similis* as a subspecies of *australis.*

HARPOBITTACUS NIGRICEPS (Selys)

Fig. 5; Plate 2, Fig. 6

Bittacus nigriceps Selys, 1868, Ann. Soc. Ent. Belg. **11**: 77.

Harpobittacus nigriceps Gerstaecker, 1885, Mitt. naturw. Ver. Greifswald **16**: 119; Esben-Petersen, 1921, Coll. Selys. **5**: 158.

Male

Head, face, rostrum, palps, and antennae black. Thorax reddish brown except for dorsal surface of prothorax and anterior portion of mesothorax, which are black. Abdomen completely black except for the dark reddish brown genitalia. Epiandrial lobes rather short and without internal tooth, apex rounded, incurved, outer surface deeply channelled.

Legs reddish brown, apex of posterior femora and almost apical ½ of anterior 2 pairs black, base and apex of hind tibiae black, while the anterior ones are almost completely black, tarsi black.

Wings with light smoky brown tinge, yellowish at base. Well-marked reddish brown pterostigma. No apical cross vein in the costal area. Subcostal cross vein of fore wing nearer to fork of *Rs* than to origin of *Rs*. Fork of *Rs*, fork of *M*, and the apical cross vein between *CuA* and *CuP* form almost a straight line. No apical cross vein between *CuP* and *1A*.

Female

Very similar to the male.

Size

Length of body, ♂ 20-21 mm, ♀ 18 mm; length of fore wing, ♂ 21-22.5 mm, ♀ 21 mm.

Type: Holotype ♂ in the British Museum (*ex* McLachlan collection).

Type locality: Australia.

VICTORIA: Toora; Lower Tarwin; Beech Forest; and Big River. QUEENSLAND (Coll. Selys).

The distribution of this species is a little confusing. It appears likely that it may be restricted to the more southern areas. In Queensland the allied *scheibeli* E.-P. occurs.

A series of 22 specimens was examined.

HARPOBITTACUS SCHEIBELI Esben-Petersen

Plate 2, Figs. 7, 8

Harpobittacus scheibeli Esben-Petersen, 1935, Vidensk. Medd. Dansk. Naturh. Foren. Kbh. **99**: 1.

Male

Head mainly black but lower portion of face and basal ½ of rostrum yellowish brown; apical portion of rostrum black, as too are the palps and antennae, so that the head appears black with the middle 1/3 yellowish brown. Thorax yellowish brown with the dorsal surface of prothorax and portion of the mesothorax almost black. Abdomen with the basal segments yellowish brown, apical segments (from 6 onwards) almost black. The hind borders of segments 2-5 are also blackish.

Epiandrial lobes of moderate size, without an internal tooth, with apex rounded, slightly incurved, and with the outer surface channelled, but not as deeply as in *nigriceps*.

Legs yellowish or reddish brown; apex of femora and tibiae blackish, tarsi also blackish. Wings with a light smoky brown tinge, yellowish at base; pterostigma well defined, reddish brown. No apical cross vein in the costal area. Subcostal cross vein, especially in hind wing, nearer to origin of *Rs* than to the fork at *Rs*. Fork of *Rs*, fork of *M*, and the apical cross vein between *CuA* and *CuP* form almost a straight line. No apical cross vein between *CuP* and 1*A*.

Female

Not examined.

Size

Length of body, ♂ 21 mm; length of fore wing, ♂ 21 mm.

Types: Holotype ♂ and paratype ♂ presumably in Esben-Petersen collection.

Type locality: Widgee, Gympie, Queensland.

QUEENSLAND: Tooloom, Jan. 1926 (H. Hacker); Mt. Tambourine, 1927 (W. Davidson); Ashgrove, Brisbane, 2.iii.1931; Stanthorpe, 1925 (E. Jarvis); Bundaberg, 21.i.1949 (R. Moller); Lawes, 7.ii.1950 (J. B. Ritson) and 3.iv.1950 (F. Kieseker).

The males from Tooloom and Mt. Tambourine each have the tip of the abdomen missing. In other characters they agree with the description of the type. There is a very damaged male specimen from Ashgrove, Brisbane, in the University of Queensland Collection.

The few records of this species indicate a distribution over coastal Queensland.

HARPOBITTACUS PHAEOSCIUS, sp. nov.

Male

Head, face, rostrum, palps, and antennae completely black. Thorax reddish brown, except for dorsal surface of prothorax and anterior portion of mesothorax, which are black. Abdomen with the basal segments reddish brown with a black apical border, segments 6 and 7 completely black, succeeding segments reddish brown. Anal appendages reddish brown. Epiandrial lobes of moderate size, without an internal tooth, with apex rounded, slightly incurved, and with outer surface deeply channelled.

Legs reddish brown, apex of femora and base and apex of tibiae blackish, tarsi blackish.

Wings with a light brown, smoky tinge, yellowish at base. Well-marked reddish brown pterostigma. No apical cross vein in costal area. Subcostal cross vein, especially in hind wing, nearer to origin of *Rs* than to the fork of *Rs*. Fork of *Rs*, fork of *M*, and the apical cross vein between *CuA* and *CuP* do not form a straight line, the cross vein being too basad. No apical cross vein between *CuP* and 1*A*.

Female

Differs from male only in abdominal coloration. The 1st 5 segments are a deep reddish brown, so that the black 6th and 7th segments are not as conspicuous as in the male.

Size

Length of body, ♂ 17 mm, ♀ 17 mm; length of fore wing, ♂ 17.5-18.5 mm, ♀ 17.5 mm.

Types: Holotype ♂, allotype ♀, and paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality: Pemberton, W.A., Nov. 1936 (K. R. Norris).

WESTERN AUSTRALIA: Pemberton; Glen Forest, 1.xii.1933 (K. R. Norris); King George Sound.

In the Division of Entomology Museum, C.S.I.R.O., Canberra, are 3 males and 2 females from the type locality and a single specimen from each of the other two localities. The species can be separated from *similis* E.-P., the other Western Australian species, by the absence of the apical cross vein between *CuP* and 1*A* and by the male genitalia. The coloration of the body and legs also differs.

ACKNOWLEDGMENTS

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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—*Chorista australis* Klug, ♂, Blundells, A.C.T. × 2.

Fig. 2.—*Chorista australis luteola* (Westwood), ♂, Hornsby, N.S.W. × 2.

Fig. 3.—*Taeniochorista pallida* Esben-Petersen, ♂, Albert River, Queensland. × 2.

Fig. 4.—*Nannochorista holostigma* Tillyard, ♂, Lake St. Clair, Tas. × 3.

Fig. 5.—*Nannochorista holostigma* Tillyard, ♂, Cradle Mountains, Tas. × 3.

Fig. 6.—*Austrobittacus anomalus*, sp. nov., ♀, paratype, Olsen's Caves, Queensland. Natural size.

Plate 2

Fig. 1.—*Harpobittacus australis australis* (Klug), ♂, collected in spring, Blundells, A.C.T. Natural size.

Fig. 2.—*Harpobittacus australis australis* (Klug), ♂, collected in autumn, Blundells, A.C.T. Natural size.

Fig. 3.—*Harpobittacus tillyardi rubricatus*, subsp. nov., ♂, holotype, Trangie, N.S.W. Natural size.

Fig. 4.—*Harpobittacus tillyardi rubricatus*, subsp. nov., ♀, Trangie, N.S.W., showing shortened wings with rounded apices. Natural size.

Fig. 5.—*Harpobittacus tillyardi tillyardi* Esben-Petersen, ♂, Sydney, N.S.W. Natural size.

Fig. 6.—*Harpobittacus nigriceps* (Selys), ♂, Big River, Vic. Natural size.

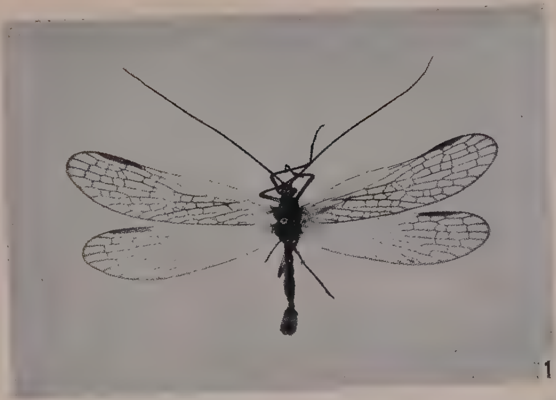
Fig. 7.—*Harpobittacus scheibeli* Esben-Petersen, ♂, Lawes, Queensland. Natural size.

Fig. 8.—*Harpobittacus scheibeli* Esben-Petersen, ♂, Bundaberg, Queensland. Natural size.

LIST OF SPECIES

Genus *Apteropanorpa*
A. tasmanica Carpenter 145
Genus *Austrobittacus*
A. anomalus, sp. nov. 157
Genus *Austromerope*
A. poultoni Killington 145
Genus *Chorista*
C. australis Klug 146
C. australis luteola (Westwood) .. 148
C. ruficeps (Newman) 149
Genus *Harpobittacus*
H. australis australis (Klug) .. 159
H. australis rubripes, subsp. nov. .. 160
H. nigriceps (Selys) 163
H. phaeoscius, sp. nov. 165
H. scheibeli Esben-Petersen 164
H. similis Esben-Petersen 163
H. tillyardi albatus, subsp. nov. .. 162
H. tillyardi rubricatus, subsp. nov. .. 160
H. tillyardi tillyardi Esben-Petersen .. 161
Genus *Kalobittacus*
K. microcercus (Gerstaecker) .. 155
Genus *Nannochorista*
N. dipteroides dipteroides Tillyard .. 152
N. dipteroides eboraca Tillyard .. 152
N. holostigma Tillyard 153
N. maculipennis Tillyard 154
Genus *Taeniochorista*
T. pallida Esben-Petersen 150

AUSTRALIAN MECOPTERA OR SCORPION-FLIES



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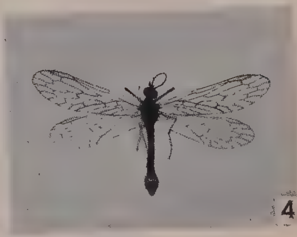

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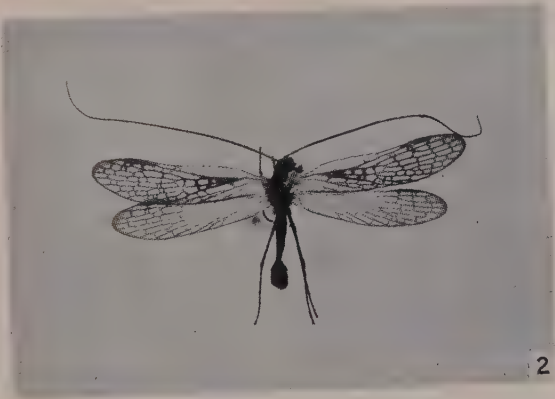

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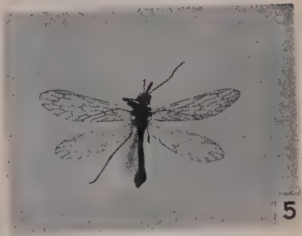

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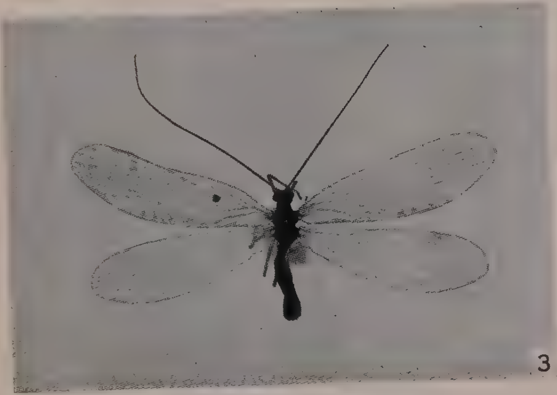

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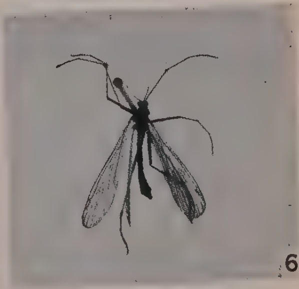

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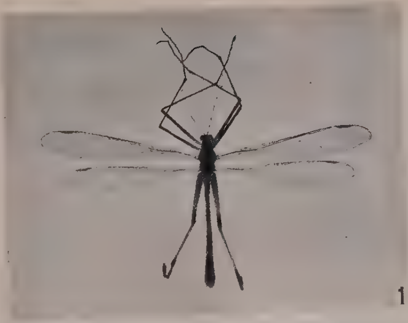

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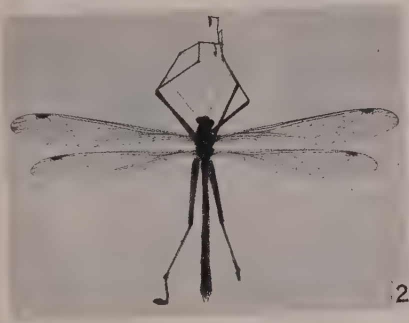

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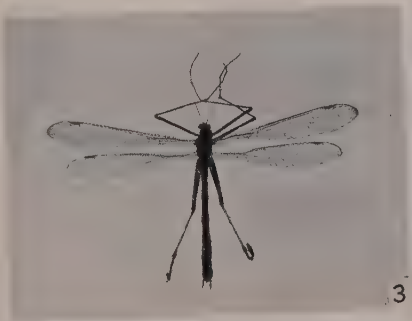

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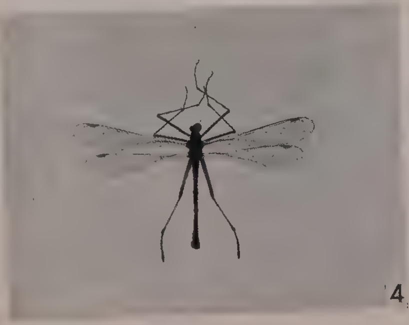

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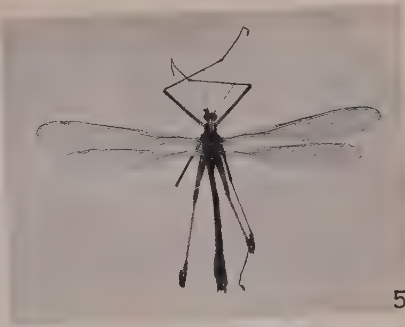

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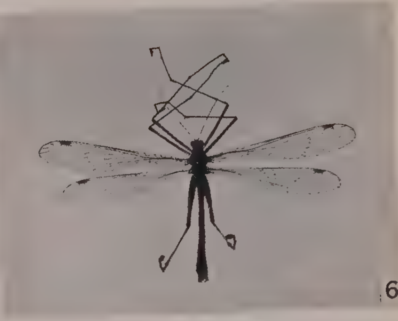

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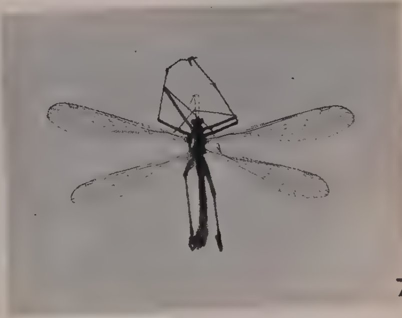

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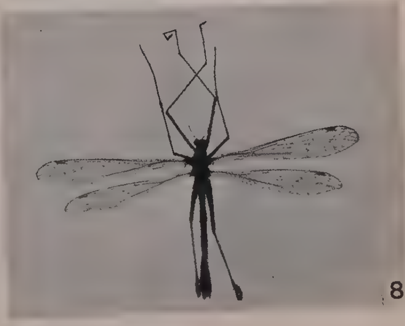

8

SPECIES OF THE SUBFAMILY PHYTOSEIINAE (ACARINA : LAELAPTIDAE) FROM AUSTRALIA

By H. Womersley*

[*Manuscript received August* 31, 1953]

Contents

Summary	169
Introduction	169
General characters	170
Key to genera of the subfamily Phytoseiinae	170
Genus *Typhlodromus* Scheuten	172
Key to species of the genus *Typhlodromus*	172
Genus *Blattisocius* Keegan	184
Genus *Kampimodromus* Nesbitt	185
Genus *Phytoseius* Ribaga	187
Genus *Amblyseius* (Koch)	188
Key to species of the genus *Amblyseius*	190
References	191
List of species	191

Summary

Twelve species of mites belonging to the subfamily Phytoseiinae (Laelaptidae) predatory on phytophagous acarids of the families Tetranychidae, Eriophyidae, and probably Pyemotidae are recorded for the first time from Australia. The species are:

Typhlodromus fallacis (Garman 1948); *T. cucumeris* Oudemans 1930; *T. bellinus,* sp. nov.; *T. longispinosus* Owen Evans 1952; *T. nesbitti,* sp. nov.; *T. victoriensis,* sp. nov.; *T.* (*Neoseiulus*) *reticulatus* Oudemans 1930; *T.* (*Neoseiulus*) *bakeri* (Garman 1948); *Blattisocius tineivorus* (Oudemans 1929); *Kampimodromus australicus,* sp. nov.; *Phytoseius macropilis* (Banks 1909) = *spoofi* (Oudemans 1915); and *Amblyseius obtusus* Berlese 1889 (ex Koch 1839).

For the guidance of Australian workers, figures of the species recorded are given, drawn from the specimens studied. Keys to the known genera and species of *Typhlodromus* Oudemans and the species of *Amblyseius* Berlese are also given.

Introduction

The mites of this subfamily are of considerable economic importance in that they are predators on the eggs and adults of the injurious mites belonging to the Tetranychidae and Eriophyidae, and probably also on certain species of Pyemotidae.

No species hitherto have been recorded from Australia, but of recent years, because of their biological importance, considerable attention has been devoted

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* South Australian Museum, Adelaide.

to their study in other parts of the world. Most notable of these studies from a taxonomic aspect is that of H. H. Nesbitt (1951) of Canada, who reviewed the world species, including the many previously described by Oudemans. The basis of specific separation adopted by Nesbitt was based on that devised by Garman (1948) and this has been since used by other workers in America and England. As described later, it is mainly concerned with the setation of the dorsal and ventral surfaces.

The 12 species recorded in this paper are based on material in the South Australian Museum collection and forwarded to me for determination over a period of years by various State Departments of Agriculture, and by the C.S.I.R.O.

GENERAL CHARACTERS

These predacious acarids are rather lightly chitinized and of general laelaptid facies, with very few specific characters. They are usually found in association with certain families of phytophagous mites. They are relatively small in size, from 300 to 600 μ in length.

The dorsal shield is entire and covers the whole dorsum except for a narrow border of cuticle. It is furnished with a variable number of fine to serrate setae, the pattern of which is of generic and specific value. In the more simple arrangements of setae, there is a dorsal longitudinal series of 6 pairs, including the 2 vertical setae, then a lateral series of 4-12 setae on each side, and between the dorsals and laterals are 2 median setae on each side. In addition there are 1 or more setae on the cuticle on each side of the dorsal shield. The system of numbering these setae, as devised by Garman (1948) and now generally adopted, is explained in some of the accompanying figures.

Ventrally in the female there is a sternal shield generally wider than long and bearing normally 3 pairs of setae and 2 pairs of pores; occasionally the 3rd pair of setae are separated from the shield. The metasternal shields are present, generally small and furnished with the usual setae. The genital shield has a truncate posterior margin and carries only 1 pair of setae. The combined ventral and anal shields are somewhat narrow, being scarcely if at all wider than the genital shield, and usually have 2-4 pairs of setae, a pair of pores on the ventral portion, and the 3 anal setae. Behind coxae IV are 1 or 2 metapodal shields. In the male the sterno-genital shields are combined but distinctly separated from the ventri-anal, which is widened behind coxae IV, roughly triangular in shape. The chelicerae of the female are simple with few teeth, and in the male the movable finger is provided with a somewhat T-shaped spermatophore carrier.

The genera at present placed in the subfamily, and all of which will possibly be found later to occur in Australia, can be keyed as follows:

KEY TO GENERA OF THE SUBFAMILY PHYTOSEIINAE

1. Some (L_4, L_6, L_8) of the dorsal setae long and whip-like, others minute; all smooth. Genus *Amblyseius* Berlese 1914. 2

No such specially long setae, or with more than 3 pairs of long setae. Most dorsal setae smooth, although some of the posterior marginal ones lightly pectinate. .4

Many dorsal setae distinctly pectinate or serrate. 7

2 (1). Ventri-anal shield usually with breadth and length equal, and remote from the posterior margin of the genital shield. ....Subgenus *Seiopsis* Berlese 1923
Ventri-anal shield larger, wider than long or its width and length unequal......3
3 (2). Ventri-anal shield much wider than genital.................................. Subgenus *Amblyseius* sens. str. Berlese 1914
Ventri-anal shield not conspicuously wider than genital...................... Subgenus *Amblysiopsis* Garman 1948
4 (1). With only 14 pairs of dorsal setae, D_5 and M_2 being absent, and D_4 and L_4 considerably longer than other dorsal setae. In the female, the ventri-anal shield with only 1 pair of pre-anal setae............Genus *Phytoseiulus* Evans 1952
With 17 or 18 pairs of dorsal setae, D_5 and M_2 present. Ventri-anal shield of female with at least 3 pairs of pre-anal setae. D_4 and L_4 normal............ Genus *Typhlodromus* Scheuten 1857
With more than 25 pairs of dorsal setae; ventri-anal shield of female with or without pre-anal setae 5
5 (4). Both fingers of chelicerae of approximately equal length....................6
Fixed finger of chelicerae only about 1/3 length of movable finger.............. Genus *Blattisocius* Keegan 1944
6 (5). Ventri-anal shield of female small and without pre-anal setae................ Genus *Garmania* Nesbitt 1951
Ventri-anal shield large and with 4 pairs of pre-anal setae.................... Subgenus *Paragarmania* Nesbitt 1951
7 (1). Dorsum smooth or only lightly imbricate, lateral setae noticeably pectinate, others may be...........................Genus *Kampimodromus* Nesbitt 1951
Dorsum distinctly rugose 8
8 (7). Lateral setae long, not leaf-like, serrate, or thorny. .Genus *Phytoseius* Ribaga 1904
All dorsal setae leaf-like and serrate..........Genus *Kleemannia* Oudemans 1930

Of these genera only *Typhlodromus, Blattisocius, Kampimodromus, Phytoseius,* and *Amblyseius* are so far known to occur in Australia.

The genus *Kleemannia* Ouds. 1930, based on *Zercon parvidus* Koch 1839, is doubtfully to be placed in the Phytoseiinae, even if it is a good genus. Garman (1948) and Vitzthum (1941) admitted it, but it was entirely ignored or has been overlooked by Baker and Wharton (1952).

By far the largest number of described species belong to the genus *Typhlodromus* and, for the guidance of Australian workers, a key to the species based on the works of Garman (1948), Nesbitt (1951), and Dr. Owen Evans (1953) is given. A key to the known species of *Amblyseius* is also given.

The species now recorded are refigured from Australian material, but for figures of the other species, all of which probably will be found here, students are referred particularly to the papers by Nesbitt (1951), Evans (1952*a*, 1952*b*, 1953), and Cunliffe and Baker (1953).

The genera included herewith are after Vitzthum (1940-43), who regarded them collectively as only a subfamily of the Laelaptidae. Baker and Wharton (1952), however, included a number of other genera in this subfamily, which they placed as a subfamily of the Phytoseiidae, along with the subfamily Podociniinae.

In the last subfamily they included the genus *Blattisocius,* which is more probably placed in the Phytoseiinae as understood by Vitzthum.

Genus TYPHLODROMUS Scheuten

Scheuten, A., 1857, Arch. Naturgesch. 23: 111.

Genotype *Typhlodromus pyri* Scheuten 1857 (= *Gamasus vepallidus* Koch 1839).

KEY TO SPECIES OF THE GENUS TYPHLODROMUS

1. With 8 lateral setae 3
With 9 lateral setae 5
With 10 lateral setae 20
With 11 lateral setae; M_2 paired with L_9. 2

2 (1). Dorsal shield imbricate. Ventri-anal shield about twice as long as wide, with 3 pairs of pre-anal setae, the median pair of which are closest together. Larger metapodal shield lenticular, about 4 times as long as wide. . . . . *T. tiliarum* Oudemans 1930
Dorsal shield smooth. Ventri-anal shield about ½ as long again as wide, with the middle pair of pre-anal setae the widest apart. Larger metapodal shield not lenticular, about twice as long as wide. . . . . *T. nesbitti*, sp. nov.

3 (1). Setae L_6 in line with or slightly posterior to D_4. M_2, L_7, and L_8 approximately equal in length. Four pairs of pre-anal setae on ventri-anal shield. . . . . *T. conspicuus* Garman 1948
Setae L_6 in line with or posterior to D_5. Fewer than 4 pairs of pre-anal setae on ventri-anal shield 4

4 (3). Dorsal shield scabrid with M_2 and L_8 markedly longer than L_7. Three pairs of pre-anal setae on ventri-anal shield; posterior margin of this shield rounded. No macro-setae on leg IV. . . . . *T. vitis* Oudemans 1930[*]
Dorsal shield smooth with M_2 and L_7 equal. Ventri-anal shield with 2 pairs of pre-anal setae and posterior margin irregular. Macro-setae on leg IV. . . . . *T. irregularis* Evans 1953

5 (1). Setae M_2 paired with either L_7 or L_8 6
Setae M_2 either forming a triangle with 2 of the lateral setae or well removed from all other setae. 13

6 (5). Setae M_2 paired with L_7 7
Setae M_2 paired with L_8. 11

7 (6). The 6 setae of the dorsal hexagonal area, i.e. D_3, M_1, and D_4, shorter in length than the distances between their bases. 8
The above setae equal in length to the distances between their bases. . . . . *T. fallacis* (Garman 1948)

8 (7). L_1 to L_4 greater in length than the distances between their bases. . . . . *T. masseei* Nesbitt 1951
L_1 to L_4 shorter than the distances between their bases. 9

9 (8). Dorsum distinctly reticulate. Female ventri-anal shield roughly triangular and as broad as long. . . . . *T.* (*Neoseiulus*) *reticulatus* Oudemans 1930
Dorsum only lightly imbricate. 10

10 (9). Dorsal setae relatively short, except M_2 and L_9 which are subequal and at least twice as long as L_7 and L_8, M_2 slightly in front of L_7. . . . . *T. cucumeris* Oudemans 1930
Dorsal setae relatively longer, especially the laterals. M_2 equal to L_7 or L_8 and about ½ the length of L_9. M_2 posterior of L_7. . . . . *T. bellinus*, sp. nov.

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[*] *T. aberrans* Oudemans 1930 was considered by Nesbitt to be the nymph of *T. vitis* Oudemans. However, he keyed it in the *vitis* group and reproduced Oudemans' Plate 362.

11 (6). All dorsal setae exceedingly long, extending to or beyond bases of succeeding setae...12
Dorsal setae shorter, not reaching bases of succeeding setae....................
T. tiliae Oudemans 1929 (= ?*T. pyri* Scheuten 1857)

12 (11). Four pairs of pre-anal setae on ventri-anal shields. Dorsal setae extending well beyond bases of succeeding setae................*T. longipilus* Nesbitt 1951
Three pairs of pre-anal setae. Dorsal setae only reaching to bases of next setae....
T. occidentalis Nesbitt 1951

13 (5). Dorsal setae long, and longer than the distances between succeeding bases. M_2 as long as D_5 and forming a triangle with L_7 and L_8.....................
T. longispinosus Evans 1952
Dorsal setae short, and shorter than distances between succeeding bases......14

14 (13). Some of the lateral setae, L_1, L_3, L_4, L_9, and M_2, are much longer than the dorsal setae. Ventri-anal shield with 3 pairs of pre-anal setae....*T. similis* (Koch 1839)*
None of the lateral setae much longer than the dorsal setae................15

15 (14). M_2 unpaired with any lateral seta but equidistant from D_5 and L_7. Ventri-anal shield of female with 4 pairs of pre-anal setae in 2 transverse rows..........
T. pomi (Parrott 1906)
M_2 forming a triangle with L_6 and L_7 or with L_7 and L_8..................16

16 (15). Setae L_1 to L_4 at least twice as long as D_2 to D_4........................17
Setae L_1 to L_4 equal to or only slightly longer than D_2 to D_4................18

17 (16). Setae L_1 to L_4 all about twice as long as D_2 to D_4. Female ventri-anal shield with 3 pairs of pre-anal setae in almost a straight row near anterior margin........
T. finlandicus (Oudemans 1915)
Setae L_1 and L_4 about 4-5 times, and L_2 and L_3 2½ times as long as D_2 to D_4. Female ventri-anal shield with 3 pairs of pre-anal setae, the 2nd and 3rd pairs in a row midway between anterior margin and apex of anus.............
T. victoriensis, sp. nov.

18 (16). M_2 about ½ as long as L_9 and 3-4 times as long as D_5. Ventri-anal shield widest in ventral part; with the 3 pairs of pre-anal setae normally arranged..........
T. asiaticus Evans 1953
M_2 about as long as D_5 and about ¼ length of L_9.......................19

19 (18). Ventri-anal shield constricted in front of anus, and anteriorly narrower than genital; 3 pairs of pre-anal setae normally arranged..........*T. newsami* Evans 1953
Ventri-anal shield ovoid, not constricted, with the pre-anal setae long, the 2nd and 3rd pairs in a transverse row.........................*T. ovalis* Evans 1953

20 (1). M_2, L_5, and L_6 forming a triangle....*T.* (*Neoseiulus*) *tiliacolus* Oudemans 1929
M_2, L_8, and L_9 forming a triangle......................................21

21 (20). With 2 or 3 pairs of pre-anal setae in both sexes..........................22
With 4 pairs of pre-anal setae on the ventri-anal shield....................23

22. Only 2 pairs of pre-anal setae; ventri-anal shield without pores and in female sole-shaped......................*T.* (*Neoseiulus*) *soleiger* (Ribaga 1902)
Three pairs of pre-anal setae; female ventri-anal shield hexagonal..............
T. (*Neoseiulus*) *barkeri* (Hughes 1948)

23 (21). Ventri-anal shield simple but with a pair of crescent-like pores in addition to the setae.........................*T.* (*Neoseiulus*) *rhenanus* Oudemans 1905
Ventri-anal shield giving the impression of an anal shield superimposed on the larger shield.....................*T.* (*Neoseiulus*) *bakeri* (Garman 1948)

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* *Typhlodromus similis* (Koch) was figured by Cunliffe and Baker, and placed in the genus *Typhlodromus*. Nesbitt, however, considered it to be a species of *Amblyseius*.

TYPHLODROMUS FALLACIS (Garman)

Fig. 1*A, B*

Iphidulus fallacis Garman, 1948, Conn. Agric. Exp. Sta. Bull. No. 520: 13.

Typhlodromus fallacis Nesbitt, 1951, Zool. Verh. Leiden No. 12: 24; Cunliffe and Baker, 1952, Pinellos Biol. Lab. Publ. No. 1: 13.

Type in the Connecticut Agricultural Experiment Station.

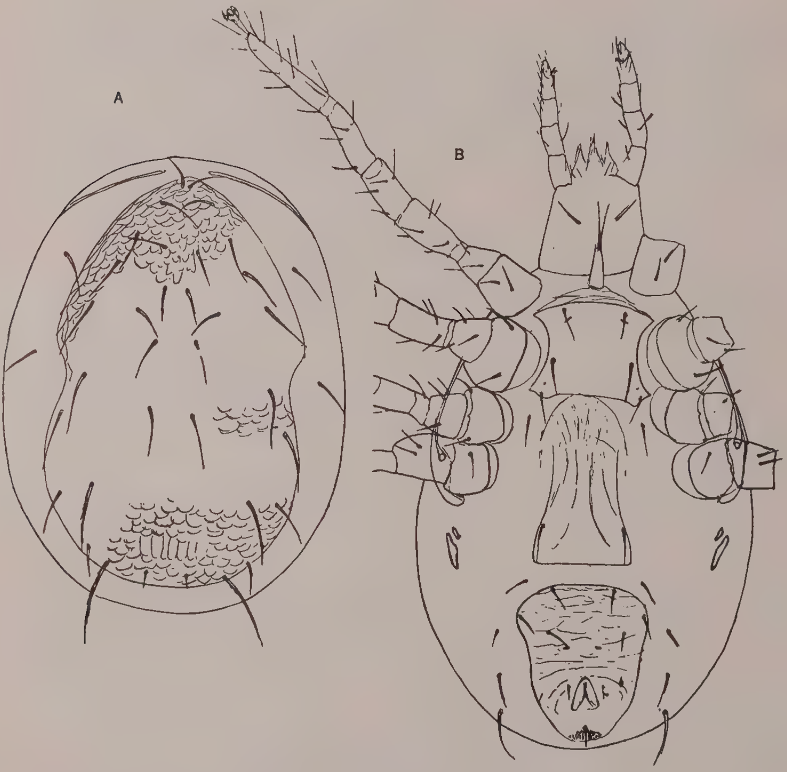

Fig. 1.—*Typhlodromus fallacis* (Garman). Female. *A*, dorsum; *B*, venter.

This species is represented in the South Australian Museum collection by a single specimen, collected from "thrips infested banana" Tweed Heads, N.S.W., 12.vii.1934, and sent from the Department of Agriculture, New South Wales. It was originally described from apple leaves, from Connecticut, U.S.A. Nesbitt (1951) recorded it from a wide variety of garden crops etc., as feeding on tetranychids, from Canada. Cunliffe and Baker also gave many American States as localities for this species. It has not so far been found in Europe.

TYPHLODROMUS CUCUMERIS Oudemans

Fig. 2*A-C*

Typhlodromus cucumeris Oudemans, 1930, Ent. Ber., Amst. 8 (172): 69-70; Nesbitt, 1951, Zool. Verh. Leiden No. 12: 23; Cunliffe and Baker, 1953, Pinellos Biol. Lab. Publ. No. 12: 15.

Type in Oudemans' collection in the Leiden Museum.

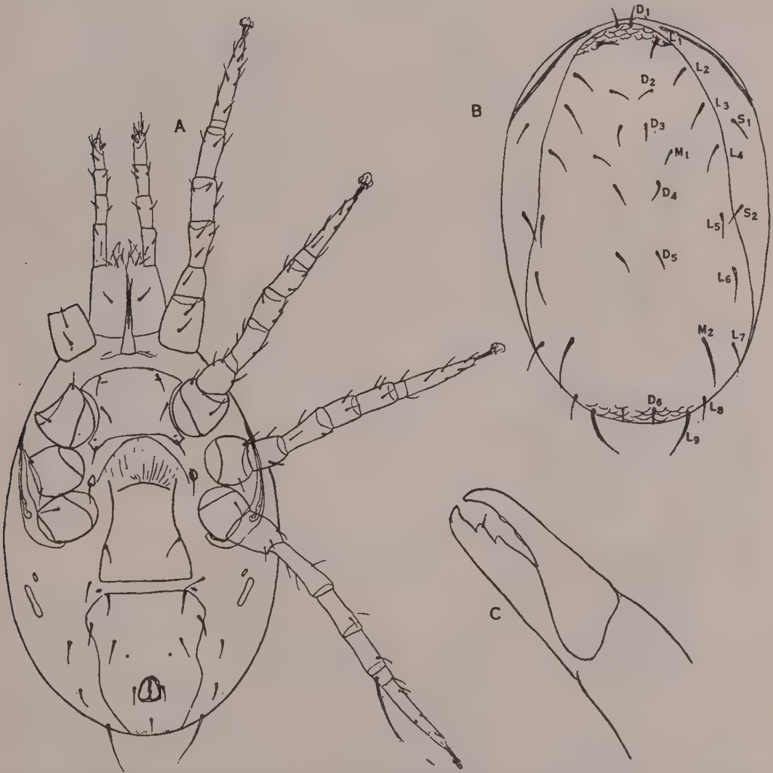

Fig. 2.—*Typhlodromus cucumeris* Ouds. Female. *A*, venter; *B*, dorsum; *C*, chelicerae.

This species has been well discussed by Nesbitt, who reproduced Oudemans' original drawings previously unpublished. Cunliffe and Baker also gave good figures which show, however, a pore alongside the setae between the genital and ventri-anal shields, as well as a small metapodal shield anterior to the larger one, both features not shown by Nesbitt. In the Australian specimens before me there is also a very distinct metasternal shield with the usual seta, the seta only of which was shown by Nesbitt and by Cunliffe and Baker. In all other respects the specimens agree with previously published figures.

The Australian specimens measure 345 μ long by 200 μ wide, and the legs are: I 273 μ long, II 247, III 247, IV 292 μ. The lengths of the dorsal setae are:

D_1 20 μ, D_2 20, D_3 14, D_4 17, D_5 17, D_6 12; M_1 14, M_2 42; L_1 17, L_2 23, L_3 23, L_4, 28, L_5 23, L_6 30, L_7 25, L_8 20, L_9 42; S_1 23, S_2 23 μ. Setae M_2 and L_9 equal and lightly barbed or serrate.

This species is represented in the South Australian Museum collection by 3 specimens from Gordo grapes, Merbein, Vic., associated with *Eriophyes vitis*. They were forwarded by the Burnley Plant Research Station, Burnley, Victoria, in June 1953.

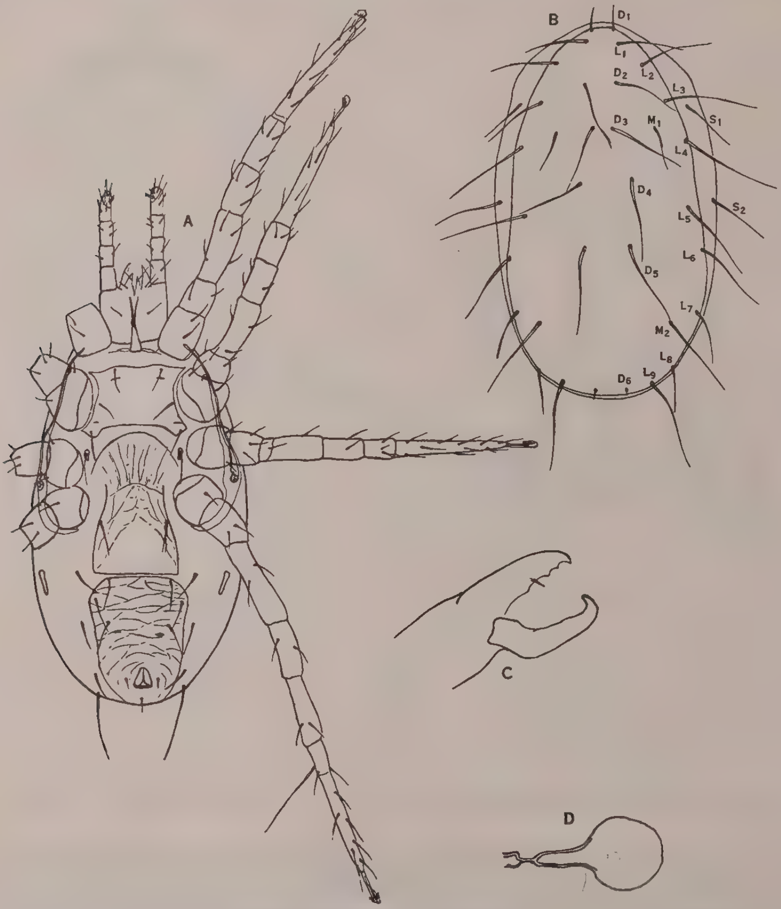

Fig. 3.—*Typhlodromus longispinosus* Evans. Female. *A*, venter; *B*, dorsum; *C*, chelicerae; *D*, spermatheca.

Oudemans' specimens were from "among numerous *Tetranychus* on *Cucumis melo* Bure (Meurthe et Moselle), France."

Nesbitt recorded it from apples and various cover crops, but not commonly, from Canada; while Cunliffe and Baker recorded it from apples in Washington, U.S.A.

TYPHLODROMUS LONGISPINOSUS Owen Evans

Fig. 3*A-D*

Typhlodromus longispinosus Owen Evans, 1952, Ann. Mag. Nat. Hist. (12) **5** (52): 413, figs. 1, 2.

Type material in British Museum, Nat. Hist.

Two slides of female specimens of this recently described species are in the South Australian Museum collection. The specimens were found on the leaves of strawberry plants received at the Plant Research Laboratory, Burnley, Vic., from Tasmania, June 1952.

Evans described and figured the species from 3 females found feeding on tetranychids on *Manihot* in Indonesia.

It will be seen from the figures now given that there is a slight difference from Dr. Evans's drawing and description of the dorsal shield in that the vertical setae (D_1) and the L_8 are longer, being respectively 25 and 42 μ, as compared with 16-17 and 15-17 μ given by Dr. Evans. This difference, however, can scarcely be regarded as important for the setal pattern and the lengths of the other setae compare favourably with the original description.

The length of the Australian specimens is 357 μ and the width 201 μ, being somewhat longer than in the Indonesian material.

The setae of the dorsal shield measure as follows: D_1 25 μ, D_2 56, D_3 60, D_4 70, D_5 70, D_6 14; M_1 40, M_2 75; L_1 56, L_2 62, L_3 78, L_4 84, L_5 70, L_6 56, L_7 75, L_8 42, L_9 84 μ.

The basal portion of tarsus of leg IV carries a long slender seta.

TYPHLODROMUS BELLINUS, sp. nov.

Fig. 4*A-D*

Description of female

Dorsal shield as figured, only lightly reticulate, with 17 pairs of setae, of which 9 are lateral. All these setae are simple, including the posterior ones. The general setal pattern is as in *T. cucumeris* Ouds., but the setae, especially the laterals, are markedly longer, as follows: D_1 25 μ, D_2 27, D_3 17, D_4 20, D_5 22, D_6 12; M_1 17, M_2 39; L_1 36, L_2 31, L_3 30, L_4 28, L_5 28, L_6 36, L_7 36, L_8 33, L_9 70; S_1 28, S_2 25 μ; M_2 is slightly posterior of L_7; L_1 to L_4 are approximately as long as the spaces between their bases; the setae of the median hexagonal area are slightly shorter than the distances between their bases; particularly noticeable is L_9, being almost twice as long as M_2. The sternal shield is wider than long, with the usual 3 pairs of setae and 2 pairs of pores; the 3rd pair of setae are on the rather truncate posterior corners of the shield between which the posterior margin is straight. The metasternal shields are distinctly visible, small, and with the usual metasternal seta. The genital shield is as usual with a single pair of setae, and truncate posterior margin. The ventri-anal shield is 130 μ long by 104 μ wide as figured, wider than the base of the genital shield, and with 3 pairs of pre-anal setae and a pair of pores posterior of the 3rd pair of pre-anal setae; posterior of the 2nd pair of pre-anal setae the shield tapers slightly to the rounded posterior. Behind coxae IV with a lenticular metapodal shield 3 times as long as wide, and a smaller adjacent shield in front of it. On the cuticle outside of the ventri-anal shield on each side are 4 setae, 1 in line with the space between genital and ventri-anal and 3 on each side of the ventri-anal; the posterior setae are about 3 times the length of the others. The peritremal shield posteriorly curves around coxae IV, and the peritreme anteriorly extends to coxae I on the dorsum. The gnathosoma and palpi are normal. The chelicerae are as figured; the fixed finger is toothless. The spermathecae lie between coxae III and IV and are shaped as in Figure 4*D*. The basi-tarsal segment of leg IV carries a long nude mastitarsala. The length of the animal measures 364 μ, width 234 μ; of leg I 299 μ, II 260, III 260, IV 351 μ.

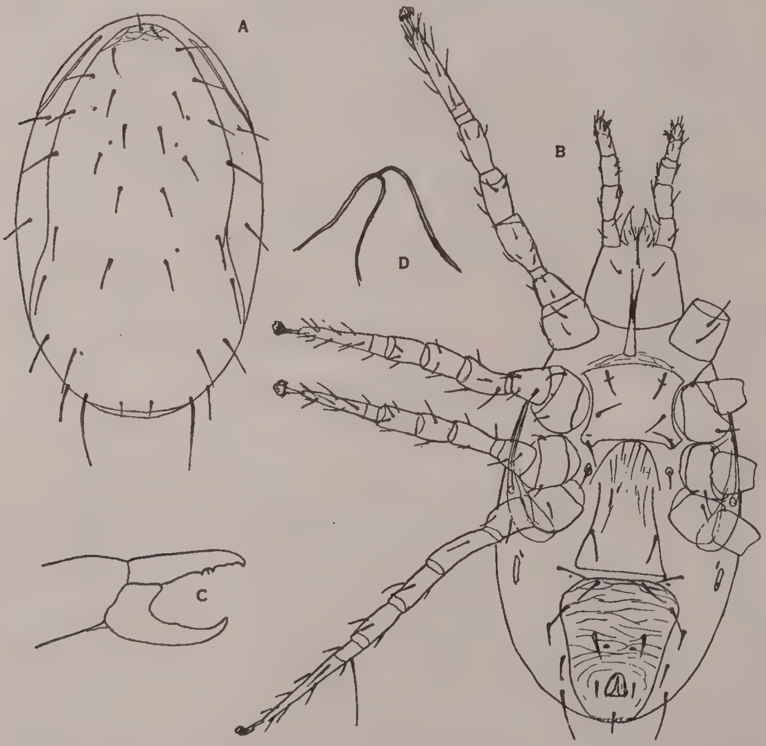

Fig. 4.—*Typhlodromus bellinus*, sp. nov. Female. *A*, dorsum; *B*, venter; *C*, chelicerae; *D*, spermatheca.

Locality

Described from 2 female specimens collected on strawberry plants imported from Tasmania, at the Plant Research Laboratory, Burnley, Vic., June 1952. The holotype and one paratype in the South Australian Museum collection.

Remarks

This is 1 of the 3 species of *Typhlodromus* so far from Australia which do not agree with any described species, and is therefore now described as new.

In the setal pattern it comes close to *T. cucumeris* Ouds., but differs in the much longer dorsal setae, especially the laterals.

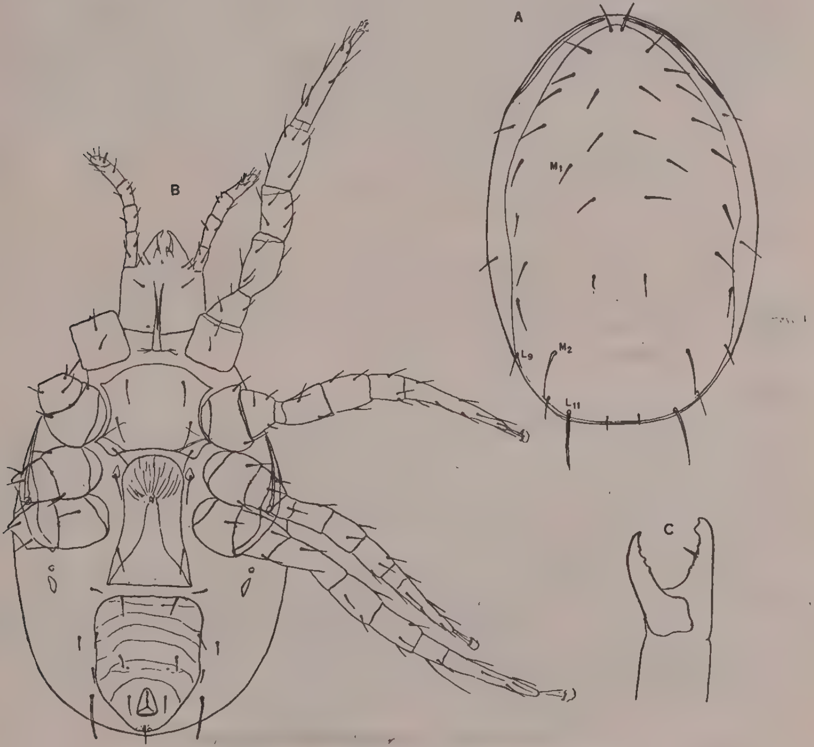

Fig. 5.—*Typhlodromus nesbitti,* sp. nov. Female. *A,* dorsum; *B,* venter; *C,* chelicerae.

TYPHLODROMUS NESBITTI, sp. nov.

Fig. 5A-C

Description of female

Shape oval, with an entire dorsal shield not quite covering the dorsum, as figured; length of idiosoma 416 μ, width 273 μ. Dorsal shield furnished with 19 pairs of setae, i.e. 6 dorsal, 2 medial, and 11 lateral; the lengths and pattern of the setae are essentially identical with those figured by Oudemans (in Nesbitt) for *T. tiliarum* Ouds.; M_2 is in line with and paired with L_9; the dorsal shield does not appear to be reticulate or imbricate and does not show the scaling indicated for *tiliarum*; D_1 28 μ, D_2 17, D_3 17, D_4 17, D_5 20, D_6 11; M_1 17,

M_2 36; L_1 20, L_2 20, L_3 22, L_4 22, L_5 25, L_6 25, L_7 20, L_8 28, L_9 22, L_{10} 22, L_{11} 56; S_1 20, S_2 20 μ. On the ventral surface the 3rd pair of sternal setae are not on separate platelets as in *tiliarum* but there is a faint line across the posterior corners of the shield and in front of the setae which might indicate an incipient break. The ventri-anal shield is 143 μ long by 110 μ wide, being shorter in proportion as compared with *tiliarum*; it carries 3 pairs of pre-anal setae which are differently arranged to those shown for *tiliarum* in that the median pair are the widest apart, being situated on the lateral edges of the shield, in contrast to *tiliarum*. The larger of the 2 metapodal shields is not long and lenticular, but only about twice as long as wide. The chelicerae are as figured, the movable finger with 3 moderately strong teeth, the fixed finger with a strong blunt subapical tooth, and then a series of minute blunt serrations. The legs are fairly thick, I 351 μ long, II 299, III 299, IV 377 μ, basal segment of tarsi IV with a moderately long seta or mastitarsala dorsally.

Locality and host

Described from a single female specimen, the holotype, in the collection of the South Australian Museum, and forwarded by the Entomological Branch, Department of Agriculture, New South Wales. It was taken from galls on tree lucerne, at Goulburn, N.S.W., 7.vi.1934.

Remarks

Hitherto the only known species of *Typhlodromus* with 11 lateral setae has been *tiliarum* Oudemans described from *Tilia* sp., Dahlem, Germany, and recorded by Nesbitt from apple, linden, and pear in Nova Scotia and New Brunswick, Canada; Nesbitt also stated that it has been recorded from Great Britain and the Netherlands.

The above new species in the dorsal setal pattern does not differ from *tiliarum*, but it lacks the imbrications shown for that species. It differs more markedly, however, on ventral features, as follows: (1) the 3rd pair of sternal setae not being off the shield; (2) the dimensions, shape, and setation of the ventri-anal shield; and (3) the size and shape of the metapodal shields.

TYPHLODROMUS VICTORIENSIS, sp. nov.

Fig. 6*A*-*D*

Description of female

Lightly chitinized. Shape ovoid, as figured. Length of idiosoma 390 μ, width 270 μ. Dorsum with 17 pairs of setae, all except the posterior pair simple. The setal pattern as figured with D_2 to D_6 and M_1 to M_2 very short; and 9 lateral setae; D_1 36 μ, D_2 8, D_3 8, D_4 8, D_5 11, D_6 6; M_1 8, M_2 11; L_1 42, L_2 20, L_3 20, L_4 36, L_5 11, L_6 14, L_7 17, L_8 14, L_9 56 (serrate); S_1 14, S_2 14 μ; dorsum not observably reticulate. Ventrally with the sternal shield slightly wider than long, with 3 pairs of setae and 2 pairs of pores, and the posterior margin lightly concave; metasternal shields only represented by the setae; genital shield as figured, with 1 pair of setae and truncate posterior margin; ventri-anal shield as figured, with the ventral (anterior) part narrower than anal portion, with 3 pairs of pre-anal setae, of which the anterior pair are at the anterior lateral corners and in advance of the other 2 pairs which are in line, a pair of pores well developed and between the pre-anal setae and the anus, the adanal setae are much shorter than the pre-anal setae; a pair of metapodal shields, about 3 times as long as wide behind coxae IV; behind each corner of the genital shield is a long seta and on each side of the ventri-anal shield are 3 setae, of which the anterior 2 are much shorter than the posterior; peritreme with the stigmata between coxae III and IV and running onto dorsum on level of coxae II, the peritremal shield extending posteriorly to behind coxae IV. Legs long and slender, I 415 μ, II 350, III 350, IV 470 μ; leg IV with a long seta dorsally on genu, tibia, and basitarsus, which setae are not tapering to a point but blunt-ended, on basitarsus 60 μ long, and tibia 42 μ, on genu 50 μ.

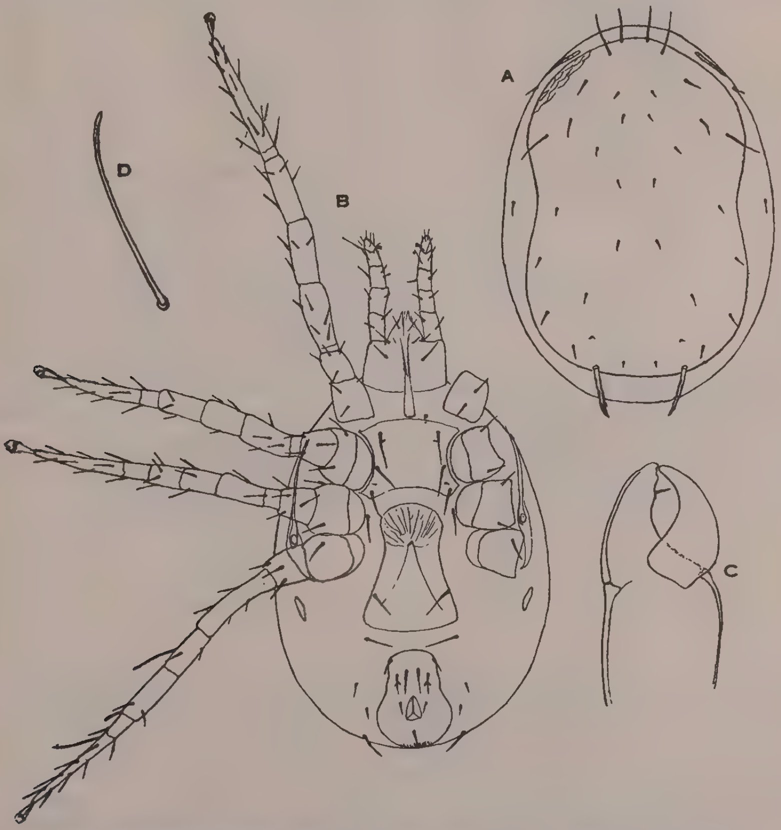

Fig. 6.—*Typhlodromus victoriensis*, sp. nov. Female. *A*, dorsum; *B*, venter; *C*, chelicerae; *D*, dorsal seta L_4.

Locality and host

Two females, holotype and paratype, in the collection of the South Australian Museum, received from the Plant Research Laboratory, Burnley, Vic., and collected from citrus leaf at Merbein, Vic., Aug. 1953 (J. R. Johnston).

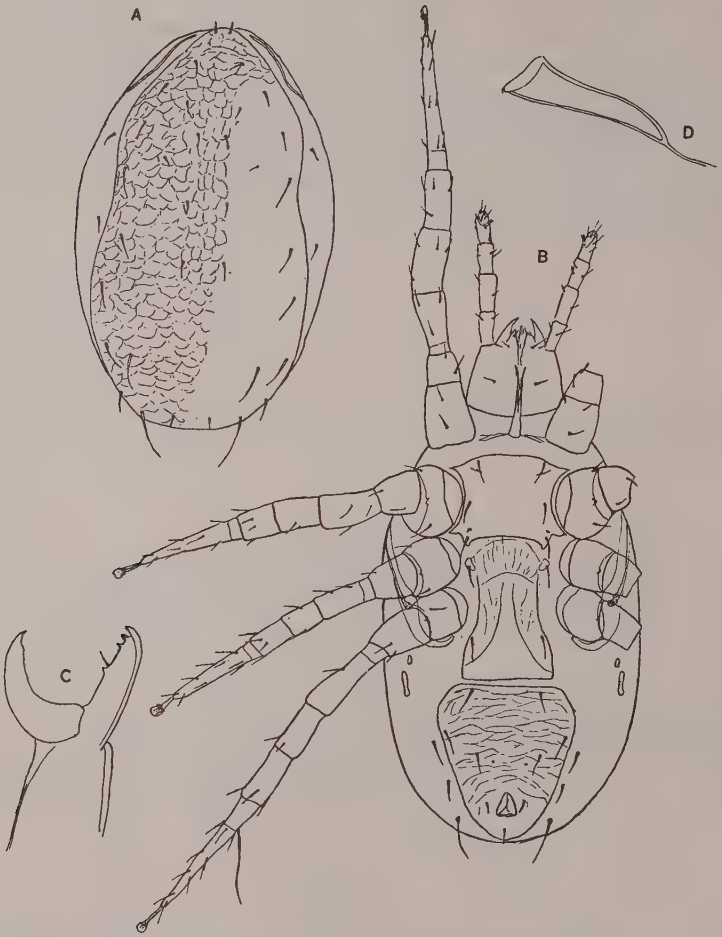

Fig. 7.—*Typhlodromus* (*Neoseiulus*) *reticulatus* Ouds. *A*, dorsum; *B*, venter; *C*, chelicerae; *D*, spermatheca.

Remarks

Near to *T. finlandicus* Ouds., but differing in the much shorter dorsal setae, D_1-D_6, M_1, M_2, and also in the arrangement of the 3 pairs of pre-anal setae on the ventri-anal shield. In the shape of the ventri-anal shield and the arrangement of the pre-anal setae thereon, it closely resembles *T. ovalis* Evans from Malaya, but these setae are shorter, and further L_1 to L_4 are about equal and short in *ovalis* but L_1 and L_4 are much longer than L_2 and L_3 in *victoriensis.*

Subgenus NEOSEIULUS Hughes

Neoseiulus Hughes, 1948, The mites associated with stored food products.

Subgenotype *Neoseiulus barkeri* Hughes 1948.

The separation of this subgenus of *Typhlodromus* was based by Miss Hughes on the greater imbrication or rugosity of the dorsum. Nesbitt (1951), however, pointed out that no very clear-cut separation on this feature was possible and added to it the presence of 10 pairs of lateral setae instead of 8, 9, or 11 pairs.

Unfortunately, 1 species, *T. reticulatus* Oudemans, which he placed under *Neoseiulus,* while having a strongly reticulate dorsum, has only 9 pairs of lateral setae and would thus fall more properly into *Typhlodromus* sens. str. However, for the present I follow Nesbitt in placing it in *Neoseiulus.*

TYPHLODROMUS (NEOSEIULUS) RETICULATUS Oudemans

Fig. 7*A-D*

Typhlodromus reticulatus Oudemans, 1930, Ent. Ber., Amst. 8 (172): 70-2.
Typhlodromus (*Neoseiulus*) *reticulatus* Nesbitt, 1951, Zool. Verh. Leiden No. 12: 37; Cunliffe and Baker, 1953, Pinellos Biol. Lab. Publ. No. 1: 16.

Type in Oudemans' collection in Leiden Museum.

Three females in the collection of the South Australian Museum were received from the Plant Research Laboratory, Burnley, Vic., collected on the leaves of strawberry plants from Tasmania, June 1952.

The original Oudemans material was found on *Calluna vulgaris,* in the Netherlands. Nesbitt (1951) recorded it as not common in Nova Scotia, British Columbia, and California preying on tetranychids attacking strawberries and clover. Other than the original material Nesbitt stated that the only European record is a single specimen from gorse (*Ulex* sp.) in Kent, England. Cunliffe and Baker (1953) recorded it as feeding on *Tarsonemus pallidus* Banks on strawberries in California.

TYPHLODROMUS (NEOSEIULUS) BAKERI (Garman)

Fig. 8*A, B*

Seiulus bakeri Garman, 1948, Conn. Agric. Exp. Sta. Bull. No. 520: 15.
Typhlodromus (*Neoseiulus*) *bakeri* Nesbitt, 1951, Zool. Verh. Leiden No. 12: 36; Cunliffe and Baker, 1953, Pinellos Biol. Lab. Publ. No. 1: 10.

Type in Connecticut Agricultural Experiment Station Collection.

Originally described from apple bark in Connecticut, U.S.A., Nesbitt also recorded it from a similar habitat in Nova Scotia, Canada.

In the South Australian Museum it is represented by 3 specimens on 2 slides; the 2 specimens on 1 slide from "twigs of Peach, bearing eggs of the Green Peach Aphis," Bathurst, N.S.W., 12.vi.1934 (N.S.W. Dep. Agric.); the other specimen "from Galled Pear twig," Roseville, N.S.W., 16.vii.1934 (N.S.W. Dep. Agric.).

Genus BLATTISOCIUS Keegan

Blattisocius Keegan, 1944, J. Parasit. **30** (3): 181-3.

Genotype *Blattisocius triodens* Keegan 1944 (= *Typhlodromus tineivorus* Oudemans 1929).

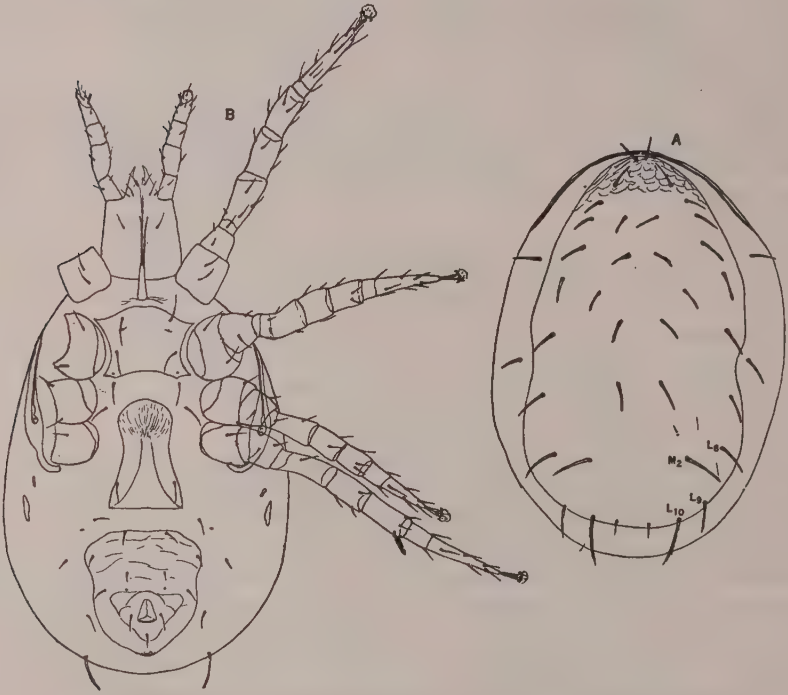

Fig. 8.—*Typhlodromus* (*Neoseiulus*) *bakeri* (Garman). *A*, dorsum; *B*, venter.

BLATTISOCIUS TINEIVORUS (Oudemans)

Fig. 9*A-C*

Typhlodromus tineivorus Oudemans, 1929, Ent. Ber., Amst. **8** (170): 34-5.

Blattisocius triodens Keegan, 1944, J. Parasit. **30** (3): 181-3. (Type in Keegan collection.)

Typhlodromus tineivorans Hughes, 1948, The mites associated with stored food products: 144-6.

Typhlodromus tineivorus Cunliffe and Baker, 1953, Pinellos Biol. Lab. Publ. No. 1: 8, fig.

Type material in Oudemans' collection in Leiden Museum.

This species is commonly found in insect cultures, and has been reported from cultures of *Sitotroga cerealella* from Illinois (Nesbitt), from cultures in wheat (Oregon) and barley (N. Dakota) (Cunliffe and Baker), and from food infested with *Ephestia, Sitotroga,* and *Plodia* from England (Hughes).

In the South Australian Museum collection are specimens from a culture of *Rhizopertha* from Canberra, A.C.T., 12.xii.1944 (coll. F. J. Gay) and from chaff, from Adelaide, S.A., May 1935 (coll. H.W.).

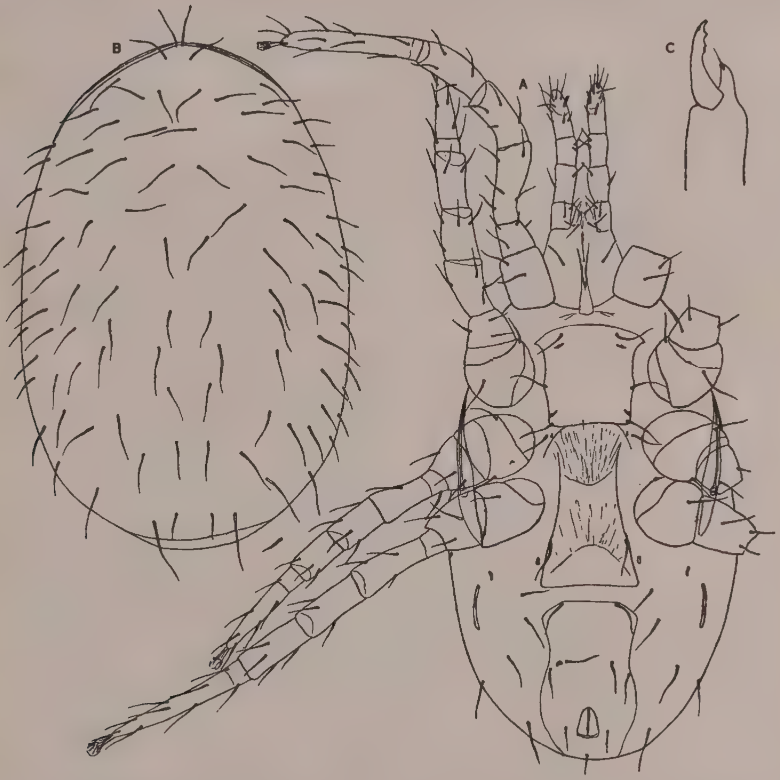

Fig. 9.—*Blattisocius tineivorus* (Ouds.). *A*, venter; *B*, dorsum; *C*, chelicerae.

Genus KAMPIMODROMUS Nesbitt

Kampimodromus Nesbitt, 1951, Zool. Verh. Leiden No. 12.

Genotype *Typhlodromus elongatus* Oudemans 1930.

KAMPIMODROMUS AUSTRALICUS, sp. nov.

Fig. 10*A*, *B*

Description of female

Shape oval, with entire dorsal shield, not quite covering dorsum, as figured; length of idiosoma 390 μ, width 260 μ; with 20 pairs of setae on shield, i.e. 6 dorsals, 2 medials, and 12 laterals, these setae are all fairly thick and lightly serrate as specified by Nesbitt for his genus *Kampimodromus*; the lengths of the dorsal setae are: D_1 22 μ, D_2 17, D_3 17, D_4 22, D_5 25, D_6 17; M_1 17, M_2 36; L_1 20, L_2 20, L_3 20, L_4 22, L_5 22, L_6 25, L_7 25, L_8 25, L_9 28, L_{10} 31, L_{11} 22, L_{12} 44; S_1 17, S_2 17 μ; L_1 to L_7 are all anterior of the constriction of the shield, and L_6 and L_7 form a diagonal line with M_1; M_2 is paired with L_{10}. On the ventral surface the sternal shield is about as wide as long with 3 pairs of setae and concave posterior margin; the metasternal shields are absent and only represented by the seta; genital shield with truncate posterior margin and 1 pair of setae; ventri-anal shield as figured, twice longer than wide, with 4 pairs of pre-anal setae; metapodal shields about 3 times as long as wide; on the cuticle on each side of ventri-anal shield with 3 setae, the posterior longer than the others and slightly serrate, a small seta on each side between ventri-anal and genital shields. Peritremal shields slightly rounding coxae IV, and peritreme anteriorly extending on to dorsum and almost meeting in the midline. Legs fairly slender, I 286 μ long, II 247, III 247, IV 325 μ; tarsi IV without any long seta. Structure of chelicerae not observable.

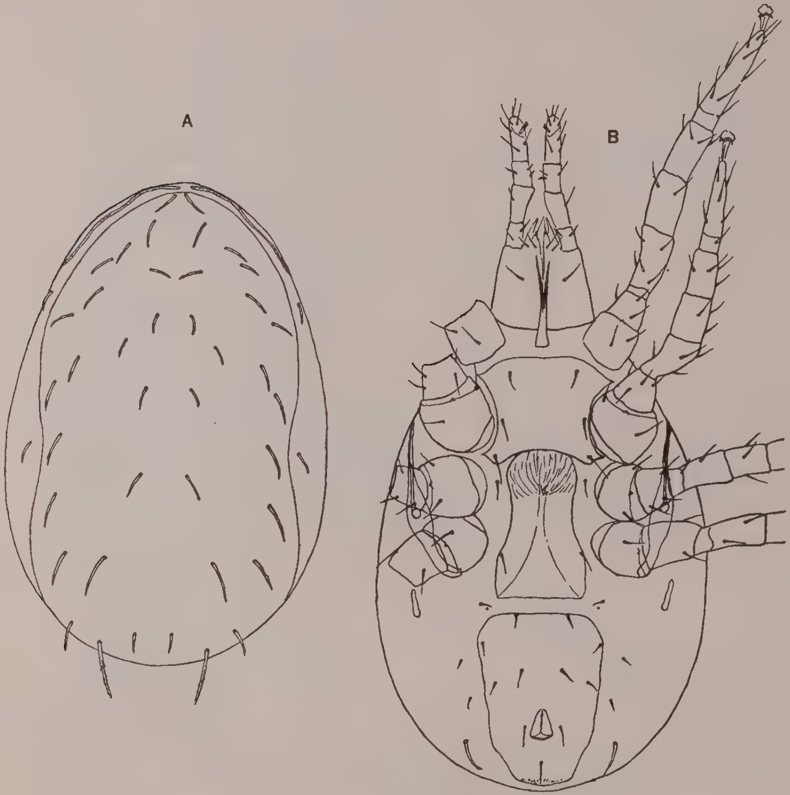

Fig. 10.—*Kampimodromus australicus*, sp. nov. *A*, dorsum; *B*, venter.

Locality and host

Described from a single specimen, the holotype, in the collection of the South Australian Museum from "under *Lecanium* scale on *Euonymus* at Bathurst, New South Wales, 19th June, 1934" and sent by the Department of Agriculture, N.S.W.

Remarks

In the nature of the dorsal setae this species falls into the genus *Kampimodromus* Nesbitt 1951. It differs, however, from the 4 species Nesbitt referred to his genus, namely *elongatus* (Ouds. 1930), *heveae* (Ouds. 1930), *hevearum* (Ouds. 1930), and *transvaalensis* Nesbitt 1951, in the greater number of dorsal setae, *elongatus* having the next largest number, 17 pairs. In these other species the dorsal and median setae are much shorter than the laterals, whereas in *australicus* they are not much so. In having 4 pairs of pre-anal setae on the ventri-anal shield *australicus* agrees with *transvaalensis*.

Genus PHYTOSEIUS Ribaga

Phytoseius Ribaga, 1904, Riv. Pat. Veg., Portici **10** (2): 177.

Genotype *Gamasus plumifer* Canestrini & Fanzago 1876.

PHYTOSEIUS MACROPILIS (Banks)

Fig. 11*A*-*H*

Sejus macropilis Banks, 1909, Proc. Ent. Soc. Wash. **11**: 135.
Seiulus spoofi Oudemans, 1915, Ent. Ber., Amst. **4** (83): 184.
Seiulus spoofi Oudemans, 1915, Arch. Naturgesch. 81A (1): 161-5, figs. 120-7.
Phytoseius spoofi (Oudemans) Nesbitt, 1951, Zool. Verh. Leiden No. 12: 57.
Phytoseius macropilis (Banks) Cunliffe and Baker, 1953, Pinellos Biol. Lab. Publ. No. 1: 22 figs.

Location of type unknown.

Specimens in the South Australian Museum collection were received from the Department of Agriculture, N.S.W., and found on *Syncarpia laurifolia,* North Ryde, N.S.W., 9.vii.1934, and on grape vine with eriophyids, at Rylestone, N.S.W., 12.iv.1934.

This species is known from Finland on *Salix* (Oudemans), from oak, sassafras, and beech in America, and from Hawaii. It is a predator on Tetranychidae and Eriophyidae.

As to the identification of the above material a careful study of the ventri-anal shield shows that there are 3 pairs of pre-anal setae present and only 1 pair, very lateral, between the posterior margin of the genital and the anterior corners of the ventri-anal whereas in the figures published by Oudemans, Nesbitt, and Cunliffe and Baker there are 2 setae between the shields and only 2 pairs of pre-anal setae on the ventri-anal shield. Whether the presence of 3 pre-anal setae is a variation or whether the anterior margin of the ventri-anal has been incorrectly drawn by the earlier authors is uncertain, but in view of the difficulty of seeing the margin in such lightly chitinized shields as a rule, it seems more probable that the earlier figures are in this respect slightly erroneous.

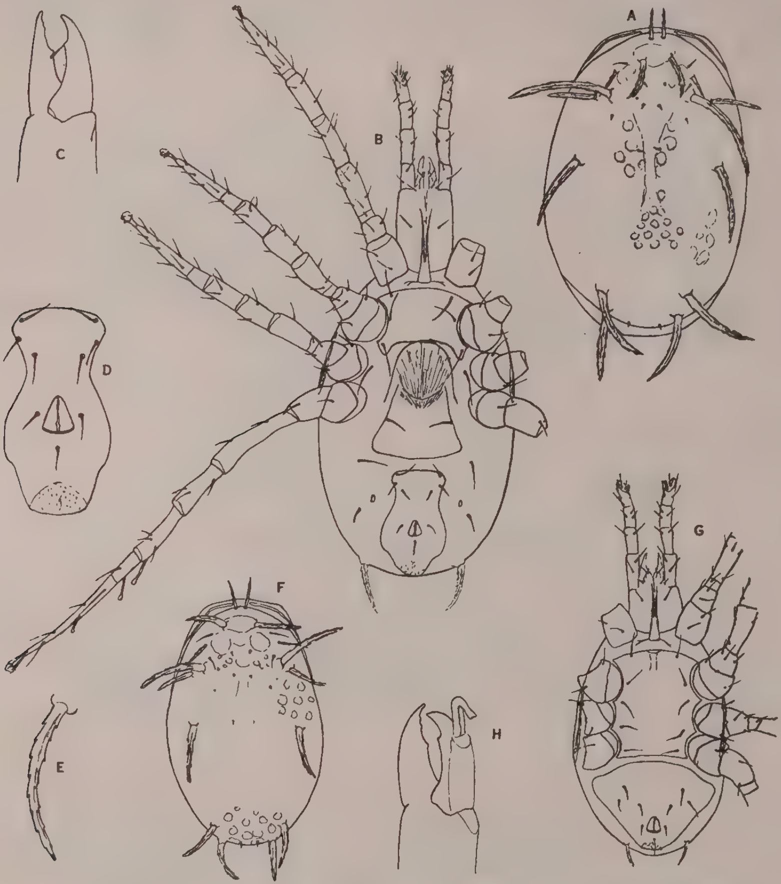

Fig. 11.—*Phytoseius macropilis* (Banks). *A-E,* female: *A,* dorsum; *B,* venter; *C,* chelicerae; *D,* ventri-anal shield; *E,* lateral seta; *F-H,* male: *F,* dorsum; *G,* venter; *H,* chelicerae.

Genus AMBLYSEIUS Berlese

Amblyseius Berlese, 1914, Redia **10**: 143.

Genotype *Seius obtusus* Berlese 1889 (= *Zercon obtusus* Koch 1839).

Amblyseius obtusus (Koch)

Fig. 12*A-D*

Zercon obtusus C. L. Koch, 1839, C.M.A. Deutschl., fasc. 27, fig. 13.
Zercon similis C. L. Koch, 1839, C.M.A. Deutschl., fasc. 27, fig. 6.

Zercon ovalis C. L. Koch, 1839, C.M.A. Deutschl., fasc. 27, fig. 11.
Zercon pallens C. L. Koch, 1839, C.M.A. Deutschl., fasc. 27, fig. 12.
Zercon mucronatus Canestrini & Fanzago, 1875, Nuovi acari italiani.
Zercon furcatus Canestrini & Fanzago, 1875, Nuovi acari italiani.
Iphis ovum Canestrini & Fanzago, 1875, Nuovi acari italiani.
Zercon obtusus Canestrini & Fanzago, 1875, Nuovi acari italiani, p. 51.
Notaspis ovum Canestrini & Fanzago, 1875, Nuovi acari italiani, p. 61.
Seius obtusus, Berlese, 1889, Acari, Myriapoda et scorpiones in Italia **54** (7).
Amblyseius obtusus, Berlese, 1914, Acari nuovi; Manip. IX: 143.

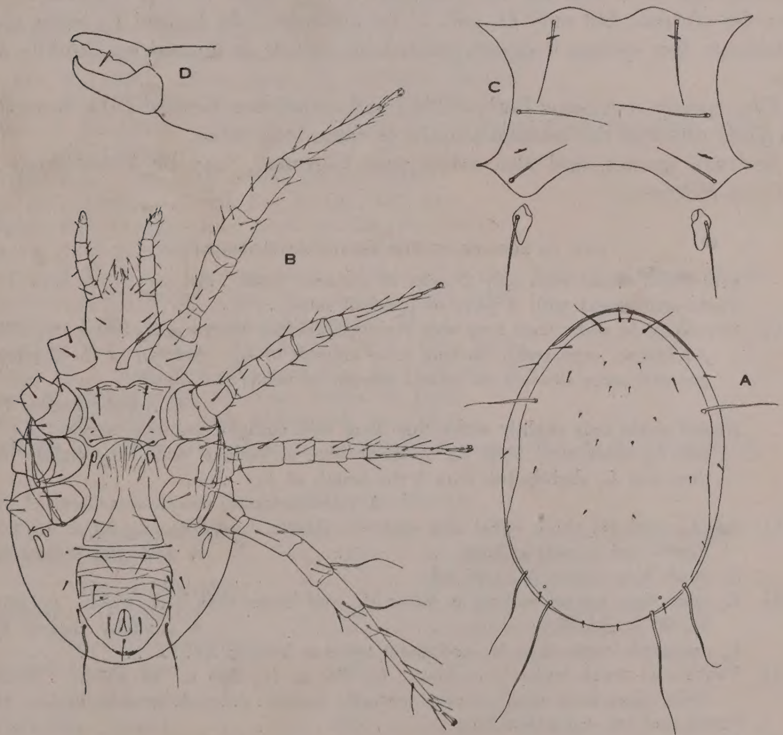

Fig. 12.—*Amblyseius obtusus* Berl. (ex Koch). Female. *A*, dorsum; *B*, venter; *C*, sternal shield; *D*, chelicerae.

N.B. The above synonymy is chiefly after Berlese in "Gli Acari," 132. Location of type unknown.

Four female specimens here referred to the type species of the genus were obtained from moss from Mt. Barker, S.A., 24.vi.1934.

The length of the idiosoma measures 390 μ and the width 260 μ. The legs are: I 494 μ long, II 390, III 390, IV 494 μ. The sternum is as figured, 118 μ wide by 84 μ long, with the seta 36 μ. The genital shield is 100 μ wide at the base. The ventri-anal shield measures 128 μ wide by 118 μ long. The anterior long lateral setae measure *c.* 80 μ, the posterior lateral 120 μ, and the posterior

160 μ; the posterior ventral setae measure 84 μ. The setae measurements agree well with those given by Berlese (1914).

Berlese (1914) described 6 species of *Amblyseius,* and 2 varieties of 1 species, mainly from moss from Italy and South America. In all he only referred to the long setae, the small dorsal setae not being mentioned or indicated in his figures. He quoted the long setae as lateral or "*L*", posterior or "*P*", and adanal or "*Ad*". According to present interpretation, his "*L*" refers to L_4 or M_2, "*P*" to L_8, while his "*Ad*" must be the long posterior ventral seta on each side of the anus. In his dorsal figures of *obtusus* and *caudatus,* D_1 (vertical setae), L_1, and L_2 are shown for *obtusus,* but only D_1 and L_1 for *caudatus.* In L_2 and L_3 being short in *caudatus,* this species is closely related to *grandis* as figured by Cunliffe and Baker.

Two species, *caudatus* Berlese 1914 and *aequipilus* Berlese 1914, described from Java, differ in the relative lengths of these long setae.

Berlese's species, and also *americanus* Garman*, may be keyed from his details as follows:

KEY TO SPECIES OF THE GENUS AMBLYSEIUS†

1. Ventri-anal shield with only 2 pairs of pre-anal setae........................2

Ventri-anal shield with 3 pairs of pre-anal setae............................3

2 (1). Sternal shield wider than long with concave posterior margin. L_8 200 μ, M_2 170 μ, *Ad* 120 μ. Apparently no long setae anterior of L_4. Anterior of the 2 pairs of pre-anal setae situated on lateral margin of ventri-anal shield..............
A. foenilis Berlese 1914

Sternal shield only slightly wider than long with straight posterior margin. L_1, L_2, and L_3 moderately long, L_8 about as long as body is wide, M_2 slightly more than and L_4 slightly less than ½ the length of L_8........................
A. (*Amblysiopsis*) *americanus* Garman* 1948

3 (1). *Ad*, L_8, and M_2 about equal and relatively shorter. *Ad* 70 μ, L_8 80 μ, M_2 80 μ. Ventri-anal as wide as long......................*A. aequipilis* Berlese 1914

L_8 much longer than M_2 and *Ad*....................................4

4 (3). L_8 more than 3 times as long as *Ad* or M_2, and longer than body width. L_8 280 μ, M_2 90 μ, *Ad* 70 μ............................*A. caudatus* Berlese 1914

L_8 not much longer than M_2 and about twice as long as *Ad*.................5

5 (4). Ventri-anal much wider than long. L_8 300 μ, M_2 260 μ, *Ad* 135 μ. Sternum wider than long, with concave posterior margin......*A. grandis* Berlese 1914

Ventri-anal not wider than long....................................6

6 (5). Sternal shield as long as wide with concave posterior margin. L_8 120 μ, M_2 119 μ, *Ad* 55 μ.................................*A. longulus* Berlese 1914

Sternum wider than long...7

7 (6). Posterior margin of sternum concave....................................8

Posterior margin of sternum straight. L_8 180 μ, M_2 115 μ, *Ad* 90 μ.............
A. obtusus var. *meridionalis* Berlese 1914

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* In the figures of *americanus* given by Garman and by Cunliffe and Baker, if the posterior-lateral long seta is considered to be M_2, then there are only 8 lateral setae, not 9 as stated by Garman, and the posterior long seta is L_8, not L_9.

† Cunliffe and Baker figured another species under the name "*Amblyseius quadripilis* (Banks)" in which only L_4 and L_8 are long, and M_2 is wanting. However, on the form of the ventral shields and the fact that the venter is laterally overlapped by the dorsal shield it does not seem to be an *Amblyseius* and probably also cannot be placed in the Phytoseiinae as restricted by Vitzthum.

8 (7). L_8 and M_2 equal, 140 μ, *Ad* 80 μ. . . . . *A. obtusus* var. *fuscus* Berlese 1914
L_8 200 μ, M_2 140 μ, *Ad* 80 μ. . . . . *A. obtusus* Berlese 1889 (ex Koch 1839)

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LIST OF SPECIES

Genus *Amblyseius*	
A. obtusus (Koch)	188
Genus *Blattisocius*	
B. tineivorus (Oudemans)	184
Genus *Kampimodromus*	
K. australicus, sp. nov.	185
Genus *Phytoseius*	
P. macropilis (Banks)	187
Genus *Typhlodromus*	
T. bakeri (Garman)	183
T. bellinus, sp. nov.	177
T. cucumeris Oudemans	175
T. fallacis (Garman)	174
T. longispinosus Owen Evans	177
T. nesbitti, sp. nov.	179
T. reticulatus Oudemans	183
T. victoriensis, sp. nov.	180